VARIATION IN THE BEHAVIOR AND FOOD SUPPLY OF FOUR NEOTROPICAL WRENS

By

KATHY WINNETT-MURRAY

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1986

ACKNOWLEDGMENTS

Many people helped me accomplish this study and I am grateful to all of them. My major advisor, John William Hardy, the other members of my advisory committee (both official and unofficial), Michael Collopy, Martha Crump, Jack Kaufmann, Peter Feinsinger, and Lincoln Brower, fellow participants in OTS 81-1, especially Jack Longino, Mary Price, Jack Putz, Jack Schultz, Nick Waser, and Nat Wheelwright, helped me to formulate ideas, hypotheses, and the approach of the study. F. Gary Stiles provided advice and encouragement. I received financial support from the Chapman Fund of the American Museum of Natural History, the Jessie Smith Noyes Foundation of the Organization for Tropical Studies, Sigma Xi grants-in-aid, and a research assistantship from the Department of Zoology, University of Florida.

The Tropical Science Center, San José, Costa Rica, granted permission to conduct research within the Monteverde Cloud Forest Preserve, and my work there was facilitated by Wolf Guindon and the Preserve staff. In addition, dozens of Monteverde residents, including the Ardens, Campbells, Cressons, Dowells, Figuerolas, Fogdens, Guindons, Hoges, James', LaVals, Mayos, Mendezes, Rockwells (all of them), Smiths, Stuckeys, Trostles, Vargases, and Wallaces, facilitated my work by generously providing access to their private land, tidbits of wren natural history, and leads on the whereabouts of nests. J. Campbell and R. LaVal allowed me to use weather information that they collected.

In the field, I was assisted by Alan Mayo, Sarah Sargent, and Alexander Vargas during nest watches, and Sarah did many of the aviary observations as well. All of the biologists who overlapped with me in Monteverde, including J. Beach, J. Bronstein, B. Busby, M. Crump, E. Dinerstein, P. Feinsinger, A. Fortenbaugh, M. Hayes, S. Jacobsen, S. Kinsman, Y. Linhart, D. McDonald, N. Nadkarni, R. Schuster, J. Shopland, J. Zarnowitz, and the Lawtons, Poundses, and Wheelwrights, helped me locate wrens and nests, build aviaries, and keep a constant supply of mealworms arriving from the U.S.. In addition, B. Busby, P. Feinsinger, D. McDonald, G. Murray, and J. Shopland collaborated with me on mist-netting and banding. I am especially grateful to Martha Crump and Peter Feinsinger, for their day-to-day interest in my work, and for their generous help and support--logistical, scientific, and emotional. While I was in Costa Rica, C. Binello, G. Kiltie, M. McDonald and V. McDonald kindly helped with logistics in Florida.

During data analysis and writing, I received valuable advice and support from all of my committee members, and from B. Busby, J. Cox, P. Feinsinger, G. Meffe, V. McDonald, J. Reiskind, J. Shopland, T. Webber, N. Wheelwright, and the participants in Eco-lunch Bunch. B. Adams, P. Ibarra, and G. Murray helped with the figures. I am grateful to the Minnos for doing more than their share of baby-trading, and to my family, the Winnetts, Sterkels, Murrays, Heineckes, Walkers, and Fichtners for their constant encouragement and interest in my work.

Finally, but most important, my husband, Greg Murray, did all of the above and much more, to enable me to complete my dissertation. He encouraged, criticized, and participated in every aspect of it from start to finish, and when the going got rough, he gave me freedom. Most

of all, during the thousand times that I wanted to quit, Greg never let me do it. Thanks, everybody!

TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	ii
ABSTRACT	vi
CHAPTERS	
I INTRODUCTION AND STUDY AREA	1
Introduction	1
Study Area	5
II COMPARATIVE BREEDING BIOLOGY OF FOUR WRENS AT MONTEVERDE	13
Methods	15
Results	17
Discussion	32
III VARIATION IN THE ARTHROPOD FOOD SUPPLY	37
Methods	37
Results	43
Discussion	96
IV VARIATION IN WREN FORAGING BEHAVIOR	100
Methods	101
Results	108
Discussion and Synthesis	155
APPENDIX SUPPLEMENTARY TABLES USED IN ANALYSIS OF ARTHROPOD DATA	167
LITERATURE CITED	171
BIOGRAPHICAL SKETCH	184

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

VARIATION IN THE BEHAVIOR AND FOOD SUPPLY OF FOUR NEOTROPICAL WRENS

By

Kathy Winnett-Murray

December 1986

Chairman: John William Hardy
Major Department: Zoology

I investigated the hypothesis that greater flexibility in foraging behavior allows the wrens in open, disturbed habitats of Monteverde, Costa Rica (House Wrens, Troglodytes aedon and Plain Wrens, Thryothorus modestus) to maintain higher reproductive rates than sympatric forest-dwelling wrens (Rufous-and-white Wrens, Thryothorus rufalbus and Gray-breasted Wood-Wrens, Henicorhina leucophrys). From 1981 - 1983 I collected data on the comparative: 1) breeding biology of the wrens, 2) spatial and seasonal variation in prey abundance, biomass, composition, clumping and substrate use in different habitats, 3) variability in the foraging behavior of wrens, and 4) responses of wrens to experimentally controlled changes in food availability.

House Wrens averaged 5 fledglings/yr compared with 1.4, 0.9, and 0.7 fledglings/yr for Plain Wrens, Rufous-and-white Wrens, and Gray-breasted Wood-Wrens, respectively. House Wren nesting success was enhanced by selection of nest sites in buildings in open habitats where predation was relatively rare. Multiple brooding, and perhaps larger clutches, were associated with greater food availability in open

habitats where arthropod biomass and composition varied less over time and space, than it did in forests. Seasonal changes in forests were more pronounced than in open habitats, and more pronounced in lower elevation woods than in higher elevation cloud forest. Open habitats supported a high diversity of arthropod orders, but the important groups in forest, larvae and arachnids, were highly seasonal and often occurred in clumps. In forests, arthropods were dispersed over a large, and highly variable array of substrates, over 40% of which were concealed.

This was correlated with greater foraging variability among forest wrens, which presumably had greater difficulty finding food, and used a greater diversity of foraging positions, attack techniques, and prey substrates than did open-habitat wrens. Capture rates varied with prey availability over different habitats. Where prey were very abundant, House Wrens could afford to specialize on larger, more profitable prey when feeding nestlings. Comparisons among species in the same habitat reduced the differences in capture rate and foraging behavior; these differences were insignificant in the aviary, where habitat structure and the prey distribution were fixed.

CHAPTER I

INTRODUCTION AND STUDY AREA

Introduction

In this study I addressed the question of how certain species exploit disturbed habitats to the extent that they achieve greater reproductive output than related species in undisturbed habitats. To do this, I studied the comparative behavior, ecology and reproductive biology of four sympatric tropical wrens, the House Wren Troglodytes aedon, (HW), the Plain Wren Thryothorus modestus, (PW), the Rufous-and-white Wren T. rufalbus, (RW), and the Gray-breasted Wood-Wren Henicorhina leucophrys, (GW) at Monteverde, Costa Rica. There they occur in habitats ranging from pasture to pristine cloud forest that differ both in seasonality (severity of dry season) and in the extent of human disturbance.

Seasonality and disturbance both result in environmental variability. Biologists have been concerned with determining how species adapt to such variability with minimal effect on their population growth rates (Whittaker and Goodman 1979). At Monteverde, both weather fluctuations and human disturbance are greater in the open, lower elevation habitats where HWs and PWs occur. These two species inhabit areas that have a long history of human disturbance. In addition, small-scale disturbances (e.g. cutting, burning, planting and harvesting of crops, grazing, and clearing of roads) are widespread, and continue to occur frequently enough to affect most individual wrens in

those habitats. Fluctuations in temperature and rainfall are greater at lower elevations as well. Thus, weather fluctuations are greater in woods at lower elevations (inhabited by RWs) than in mature cloud forest at higher elevations (inhabited by GWs).

Whittaker and Goodman (1979) predicted that species adapted to exploit fluctuating environments should exhibit: 1) opportunism, characterized by the ability to find new habitat patches, to reproduce quickly, and to disperse to new patches when local conditions deteriorate (MacArthur and Wilson 1967); 2) flexibility in their demographic characters; and 3) generalism, manifested in a greater breadth of resource use (Levins 1968, Pianka 1970, Morse 1971, 1980, Southwood 1977), as compared with species in stable, saturated environments. All of these predictions imply behavioral, as well as demographic adjustments, since patterns of reproduction and habitat use are manifested in behavior.

Many studies describe the correlations between habitats and various reproductive parameters in birds (e.g. Lack 1968, Cody 1971, Wiley 1974, Horn 1978, Ricklefs 1980) and several potential mechanisms for achieving variability in reproduction have been suggested. Birds adapted for rapid responses to ephemeral breeding conditions in arid habitats (Keast and Marshall 1954, Serventy 1971) and several "irruptive" species of New World warblers, blackbirds, and orioles respond opportunistically to highly irregular outbreaks of their insect prey (Kendeigh 1947, Orians 1961, Morse 1971, Sealy 1980). These birds are characterized by high reproductive output and extreme vagility. Many birds other than these extreme opportunists show some degree of flexibility in reproduction in response to environmental circumstances, especially food availability

(Lack 1954, Pitelka et al. 1955, Perrins 1965, Cody 1971, Howe 1976, Anderson 1977, Kluyver at al. 1977, Murray et al. 1980, Clark and Wilson 1981, Marr and Raitt 1983). After egg-laying, adjustments in reproductive commitment may be manifested through direct manipulation such as brood reduction (Howe 1976, O'Connor 1978), or through relatively subtle changes in time budgets (Murray et al. 1980, 1983, Burley 1980, Westmoreland et al. 1986), parental roles (Orians 1961, Kale 1965, Verner 1965, Wiley 1974, Wiley and Wiley 1980, Wittenberger 1982), brood protection (Bryant 1975, Murray et al. 1980), foraging effort (Root 1967, Morse 1968, Robinson 1986), or parent-offspring interactions (Ricklefs 1965, Parsons 1975, O'Connor 1978, Bechard 1983, Hagan 1986). Variability in the age of dispersal and the age of first breeding has been correlated with changing environmental conditions in a variety of birds (Selander 1964, Cody 1971, Higuchi and Momose 1981). Assistance by helpers at the nest can alter the reproductive output of a breeding pair (Brown 1978, Emlen 1978, Brown et al. 1982); the incidence of helping behavior has been related to habitat seasonality in a variety of birds (e.g. Rowley 1965, Hardy 1976, Stacey and Bock 1978, Raitt and Hardy 1979, Wiley and Rabenold 1984).

Flexibility in resource use should correlate with reproductive flexibility. Species that are particularly good colonists are often ecological generalists (Mayr 1965, Simberloff and Wilson 1969, 1970, Diamond 1975, Terborgh et al. 1978, Vassallo and Rice 1982). In addition, numerous biologists have investigated the relative degree of generalized vs. specialized foraging behavior or relative plasticity vs. stereotypy in foraging in relation to competition and species diversity in bird communities (Root 1964, Miller 1967, Morse 1971, 1974, 1977,

Krebs et al. 1972, Willis 1974, Lack 1976, Partridge 1976, Abbott et al. 1977, Stiles 1978, Martin 1981, Askins 1983, Ebenman and Nilsson 1982, Vassallo and Rice 1982, Airola and Barrett 1985). Greenberg (1983, 1984a) has demonstrated that generalist foraging patterns are influenced, in part, by psychological factors such as neophobia (fear of novel situations). He attributes the broader niche of Bay-breasted Warblers (Dendroica castanea), as compared with sympatric Chestnut-sided Warblers (D. pensylvanica) to the greater probability of Bay-breasteds approaching and investigating novel microhabitats.

Despite the vast literature that exists on the comparative foraging behavior and reproductive biology of birds, and although biologists have predicted the type of behavior that should adapt an animal for disturbed habitats, we know little about the precise role of flexible behavior patterns in the achievement of particular reproductive parameters. Consequently, we know little about the behavioral mechanisms that buffer populations against environmental fluctuations. Because tropical habitats are currently suffering unprecedented rates of disturbance by man, it will be increasingly important to understand what mechanisms are critical in determining how different species respond to habitat alterations.

My study dealt with the functional role of behavior in achieving particular life history traits in relation to habitat variability. I had two major objectives: first, to determine the relative degree of fluctuation in resource availability across different wren habitats, and second, to identify differences in the behavioral capacity of the four wrens to exploit changes in resource availability through differences in foraging behavior.

My approach to this study involves three general hypotheses based on the information discussed above:

1. Environmental variability, specifically the temporal and spatial availability of food, should vary more in open, disturbed habitats occupied by HWs and PWs than in forests occupied by RWs and GWs.

2. As a result of hypothesis 1., wrens in the open, disturbed habitats should have a higher reproductive potential than wrens in forests.

3. The higher reproductive potential of species in disturbed habitats is achieved through greater flexibility in foraging behavior. HWs and PWs should have broader niches (generalism) and greater variability in foraging behavior over time (plasticity) than RWs and GWs. This should allow a longer breeding season and larger clutches in HWs and PWs compared to RWs and GWs.

I tested these hypotheses using data collected on the:

1. Comparative reproductive biology of the four wrens.

2. Spatial and seasonal variation in food availability in the different wren habitats.

3. Comparative variability in foraging behavior of the wrens in different habitats and seasons.

4. Comparative responses of the wrens to experimentally controlled changes in food availabililty (to determine short-term variability in foraging behavior, neophobia, and foraging behavior in a controlled habitat).

Study Area

My study area included the 3500 ha Monteverde Cloud Forest Preserve and the adjacent community and farmland of Monteverde, Puntarenas Province in northwestern Costa Rica (10 18'N 84 48'W; Fig. 1-1). Monteverde lies on a plateau between 1300 and 1850 m near the crest of the Cordillera de Tilarán. The cloud forest Preserve, from 1450 to 1850 m, lies on both slopes of the divide and includes Lower Montane Rain Forest and Lower Montane Wet Forest life zones (Holdridge 1967). Diverse habitats lie within the Preserve; the terrain is cut by valleys

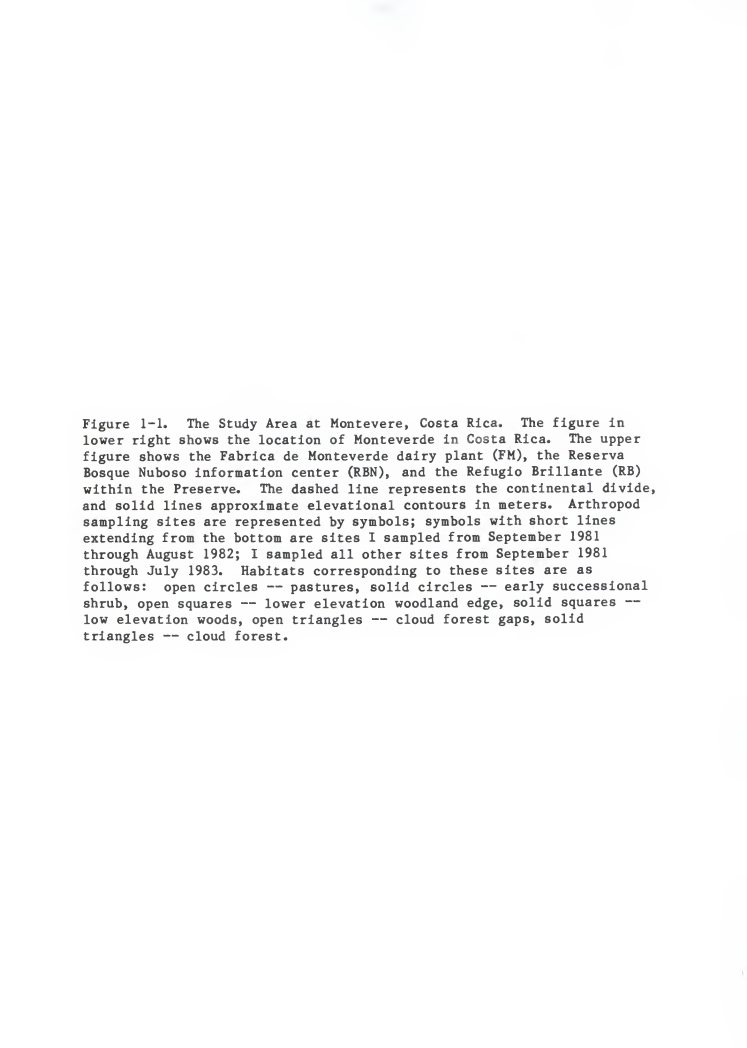
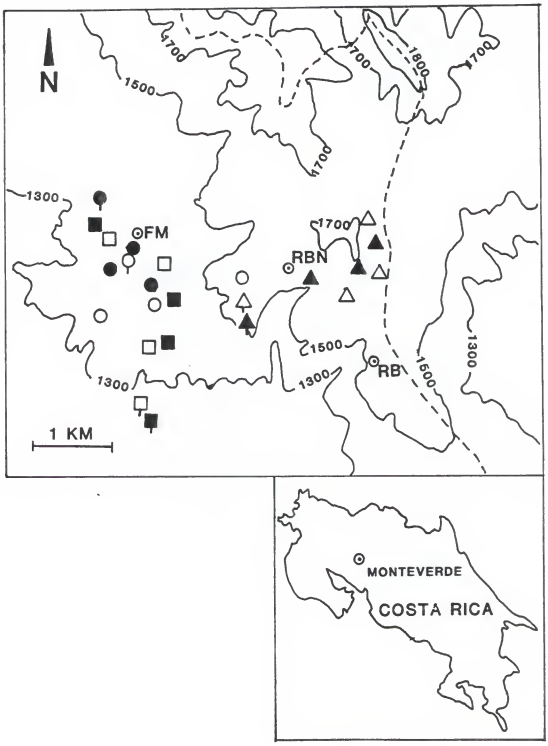


Figure 1-1. The Study Area at Montevere, Costa Rica. The figure in lower right shows the location of Monteverde in Costa Rica. The upper figure shows the Fabrica de Monteverde dairy plant (FM), the Reserva Bosque Nuboso information center (RBN), and the Refugio Brillante (RB) within the Preserve. The dashed line represents the continental divide, and solid lines approximate elevational contours in meters. Arthropod sampling sites are represented by symbols; symbols with short lines extending from the bottom are sites I sampled from September 1981 through August 1982; I sampled all other sites from September 1981 through July 1983. Habitats corresponding to these sites are as follows: open circles -- pastures, solid circles -- early successional shrub, open squares -- lower elevation woodland edge, solid squares -- low elevation woods, open triangles -- cloud forest gaps, solid triangles -- cloud forest.


N
1700
1500
1700
1800
1700
1700
1300
FM
1700
RBN
1500
RB
1500
1300
1300
1300
1 KM
MONTEVERDE
COSTA RICA

and three major rivers (R. Gaucimal, R. Peñas Blancas and R. Negro). Higher, more exposed areas tend to have a lower canopy (2-10 m), but with a dense understory and epiphytic growth. The canopy in lower, more protected areas, ranges from 10-40 m high, with a less dense understory and moderate epiphytic growth (Lawton and Dryer 1980).

The dairy-farming community of Monteverde adjoins the Preserve on the western slope and extends about 4 km to the edge of the plateau. The area includes a mosaic of habitats: scattered pastures, clearings in various stages of succession, and remnant tracts of regenerating woods. The area includes Lower Montane Moist Forest and Premontane Moist Forest life zones (Holdridge 1967). As noted by Feinsinger (1976), abundant Chorotega Amerindian artifacts suggest that humans have inhabited the area for many centuries, at least on a seasonal basis.

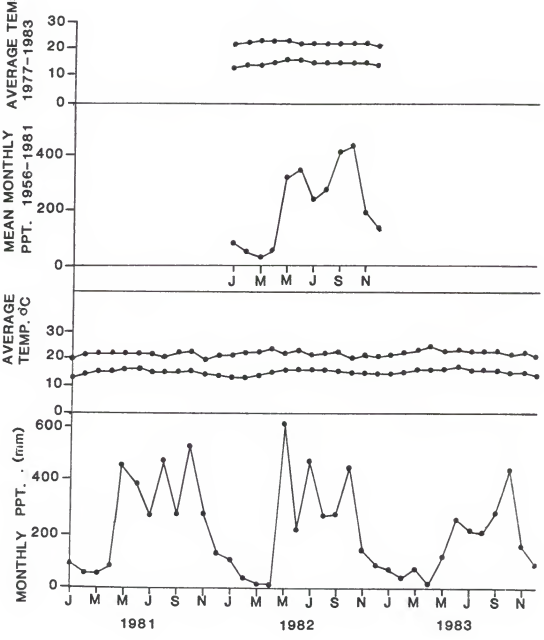
The climate of Monteverde is strongly influenced by the NE trade winds, which constantly carry moisture-laden clouds to the crest of the Cordillera. Thus, the cloud forest remains wet nearly all year (Lawton and Dryer 1980). In the lee of the winds, habitats change rapidly along a sharp moisture gradient down the Pacific slope. Elevations between 1300 and 1450 m have a more severe dry season; the woods are partially deciduous with a canopy height from 10 - 40 m and light epiphytic growth. The understory is usually a tangle of woody vines and shrubs, in contrast to the very dense foliage understory of the cloud forest. The vegetation of the area is described in detail by Lawton and Dryer (1980).

Because of the influence of Monteverde's location on its climate, the transition from wet to dry season is not as distinct as it is at lower elevations. The dry season, when there is little or no rain,

moderate wind and few clouds below 1450 m, extends from about December/January to the end of April (Fig. 1-2). The wet season usually begins in May and extends through November or mid-December; the days are characterized by heavy afternoon rains, little or no wind, and cloudy skies. Unlike the abrupt transition from dry to wet seasons in May, the transition from wet to dry (October - January) is a variable period, often with days of continuous heavy mist and high winds interspersed with occasional sunny, dry days. In some years, a brief dry and sunny spell, the veranillo, occurs in July or August. In both years of my study, precipitation had decreased markedly by December, and for my data analysis I divided the year into wet (May-November) and dry (December-April) seasons.

I obtained rainfall and temperature records from 1972-1983 from a station at 1500 m, and for 1956-1971 from a station at 1350 m (J. Campbell, pers. comm.). I gathered additional rainfall and temperature data at two sites from September 1981 - July 1983. One site was at the Monteverde Preserve field station at 1500 m, 1 km closer to the crest of the Cordillera than Campbell's station. The second was on a farm at 1350 m (R. LaVal, pers. comm.). Figure 1-2 shows average rainfall patterns for the period 1956-1981, and temperature data from 1977 to 1983 (J. Campbell, pers. comm.) along with similar data for the 2 years of this study. Weather during my study was atypical during two periods: 1) The start of the 1982 wet season in May was unusual in having the highest monthly rainfall recorded in Monteverde since 1956 and 2) 1983 was an El Niño year that was exceptionally dry. Moderate, unseasonal March rains were followed by unusually dry weather in what normally would have been the start of the wet season (May - July).

Figure 1-2. Climate at Monteverde, Costa Rica. From bottom to top, the four graphs depict: 1) total monthly precipitation (mm) for the 3 years including my study period, 1981 - 1983, 2) the minimum and maximum temperatures (^{o}C) averaged by month, from 1981 through 1983, 3) total monthly precipitation (mm) averaged for the years 1956 - 1981, and 4) minimum and maximum temperatures (^{o}C) averaged by month for the years 1977 - 1983. Data provided by J. Campbell, Monteverde, Costa Rica. Letters on the horizontal axis refer to months of the year.


AVERAGE TEMP. 1977–1983
30
20
10
0
MEAN MONTHLY PPT. 1956–1981
400
200
0
J M M J S N
AVERAGE TEMP. °C
30
20
10
0
MONTHLY PPT. (mm)
600
400
200
0
J M M J S N J M M J S N J M M J S N
1981
1982
1983

Variation in ambient temperature was slight at Monteverde, and fluctuated only 12^{o} C during my study period. Temperatures were warmer during the dry season and coolest during the misty months from October to January. Patterns during my study were typical of average fluctuations except for the warmer temperatures in 1983 that were correlated with the very dry weather in that year (Fig. 1-2).

CHAPTER II

COMPARATIVE BREEDING BIOLOGY OF FOUR WRENS AT MONTEVERDE

Wrens, except for one species (Troglodytes troglodytes) that occurs in both North America and Eurasia, are exclusively New World insectivorous passerines, especially species-rich in the neotropics (Peters 1931, AOU 1983). Tropical forms are typically monogamous and sedentary (Skutch 1960) in contrast to temperate species, which often are polygynous and migratory (Welter 1935, Kendeigh 1941, Armstrong 1955, Kale 1965, Verner 1965, Armstrong and Whitehouse 1977, Kroodsma 1977, Garson 1980). Wrens occur in nearly all habitats; in the neotropics, they range from sea-level to timberline; they inhabit tropical forest, second growth, grassland and marshes, thorny scrub, deserts and many islands; several species may occur at any given location where there is a diversity of habitats.

The nests of wrens are closed globular structures constructed by both sexes, or are cup-shaped nests placed in natural or man-made cavities. Many tropical species build several dummy or dormitory nests (Skutch 1960) in addition to the breeding nest. Some of the extra nests may be used for sleeping or to house the young after fledging. Others apparently are not used and their function remains unknown. In all wrens thus far studied, only the female incubates and broods the chicks, but both sexes may share in feeding the young. All four species I studied at Monteverde were typical of neotropical wrens in maintaining

territories and pair bonds throughout the year (Skutch 1960). Morton and Farabaugh (1979) found an RW nest in Panama with a chick of a brood parasite, the Striped Cuckoo, Tapera naevia, but no brood parasites occured at Monteverde. Helpers at the nest have been observed in several wrens, including a rare instance in the tropical House Wren (Skutch 1960).

The visually inconspicuous nature and sexual monomorphism of wrens are probably the basis for the high degree of song development found in the family (Kroodsma 1977). Females of several species have well-developed song. In PWs, for example, members of a pair engage in antiphonal duets. The function of duetting is currently under investigation (E.S. Morton, S. Farrabaugh, R. Levin, pers. comm.). PWs at Monteverde duet vigorously during territorial disputes, and they may sing either alone or together while foraging; they apparently maintain close vocal contact most of the time. Female RWs also sing, and although there are occasional bouts of overlapping song within the pair (also S. Farabaugh, pers. comm.), the male and female do not typically maintain vocal contact while foraging. The female RW's song is not as vigorous or heard as often as the male's. Similarly, female GWs sing often with their mates during territorial disputes, and occasionally while foraging or at the nest, but the songs are not always coordinated into an antiphonal duet. Of the four species studied at Monteverde, only female HWs do not sing conspicuously. In contrast to the persistent advertising song of males, female HWs, when they occasionally vocalize, utter a softer, much simpler twitter (see also Skutch 1953; Alvarez-López et al. 1984).

Eight species of wrens occur in the mountains surrounding Monteverde. Besides the four forms treated here, there are the Band-backed Wren (Campylorhynchus zonatus, confined to the wet Caribbean slope and not included in my study area), the Ochraceus Wren (Troglodytes ochraceus), a small, little known and largely arboreal resident of humid cloud forest, and two species that have recently expanded their altitudinal ranges up to the Monteverde area, the White-breasted Wood-Wren (Henicorhina leucosticta) and the Rufous-breasted Wren (Thryothorus rutilus).

The comparative studies of Skutch (1940, 1953, 1960, 1972, 1981), Selander (1964), Arnold (1966), Stiles (1983), Rabenold (1984) and Wiley and Rabenold (1984) have provided valuable information on the general biology of many Central American wrens; however, most neotropical wrens remain virtually unstudied. Previous to this study, only anecdotal information was available describing the breeding biology of PWs, RWs, and GWs. In addition, Slud (1964) and Arnold (1966) have provided some preliminary information on the habitat preferences of Thryothorus wrens in Costa Rica. The widespread tropical form of the House Wren (Troglodytes aedon musculus), however, has been studied by Haverschmidt (1952) in Suriname, Skutch (1953) in the southern lowlands of Costa Rica, and Alvarez-López et al. (1984) at a middle elevation site in Colombia. Freed (pers. comm.) also studied HWs in lowland Panama concurrent with my study. For this species then, we have comparative data on the breeding biology at other tropical locations.

Methods

I captured wrens in mist nets, weighed them with a 30 g Pesola spring scale, recorded the presence or absence of brood patches or molt,

and colorbanded each with a unique combination of leg bands for individual identification. I colorbanded nestlings between 4 and 10 days old. I banded a total of 249 wrens, representing about 40% of the individuals for which I collected foraging data, and 70% of the breeding individuals at nests I monitored. I observed nests from a concealed spot 25 m from the nest (HWs and RWs), or from within a small blind 12 - 18 m from the nest in densely vegetated habitats (PWs and GWs). I observed nests opportunistically, at all times of the day, for 1 to 4 hours at a time. When females were incubating, I recorded the length of time they spent on and off their nests, and the males' behavior near the nests. When wrens were feeding chicks, I recorded the identity of the parents as they made trips to the nest, the time intervals between trips, and the size length class and type of arthropod that was brought to the nest, following the same categories used for insect sampling (see Chapter Three, Methods).

I took the dimensions of each active nest, and recorded the construction and materials used. When I discovered a nest early in the egg-laying sequence, I weighed each egg with a 10 g Pesola spring scale. After egg-laying I checked nests every one or two days to determine the incubation (number of days elapsed between clutch completion and the day the first chick emerged) and nestling periods (number of days elapsed between emergence of the first chick and the day the last chick left the nest), and to record the nest contents. Where nests were accessible, I weighed chicks daily with spring scales until they were fully feathered, or 10 - 14 days old, to calculate growth rates. After chicks fledged, I noted the length of time they remained on the natal territory.

Results

House Wrens

Neotropical HWs, that were formerly considered a species, Troglodytes musculus, are now included in the species Troglodytes aedon, which thus has a remarkable breeding range from southern Canada south in virtually all of Central and South America including the Lesser Antilles, Trinidad and Tobago, to the Falkland Islands and Tierra del Fuego (Peters 1931: 422-427; AOU 1983). The musculus group comprises the races from southeastern Mexico to the southern extent of the species' range (Peters 1931, A.O.U. 1983). HWs occur almost everywhere that man has created any clearing; at Monteverde, HWs occupy pastures, gardens, dwellings and woodland edges up to about 1600 m, coincident with the upper extent of extensively cleared tracts. Where roadsides have opened clearings through forest at higher elevations, HWs can be found along these avenues through intact cloud forest as well (Slud 1964). A few individuals reside at the Refugio Brillante (Fig. 1-1), a small clearing once continuous with farmland but now part of the Monteverde reserve. The open land ajoining the Refugio with lower farmland has since regenerated to forest, but HWs remain in the small clearings immediately surrounding the cabin.

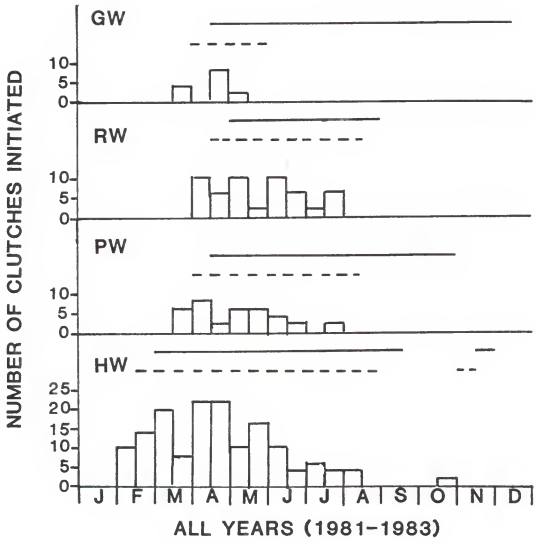
HWs are the only wrens at Monteverde that do not build a closed, globular nest. HWs build cup-shaped nests by filling any sort of natural or man-made cavity with coarse sticks and lining this cup with soft fibers, feathers, livestock hair, and bits of trash (yarn, pieces of plastic bag, etc.). Fifty-nine percent of the 39 nests I followed were on or in dwellings or milking barns. Nests on buildings were

usually placed under the eaves of the roof or in crevices in the walls, and therefore tended to be 2 to 5 m high. The other 16 nests were in or near pastures and situated as follows: 12 in holes in roadside banks (0.5 to 2 m above the road), one in a hole in a roadside fencepost (1.5 m high), one in an open crevice in the top of a stump (1 m high; the eggs in this nest flooded the first time it rained), and two at ground level in nooks at the bases of stumps.

Although the clutch sizes of tropical HWs (2-6 eggs) are smaller than those of their temperate relatives (typically 4-8 eggs; Skutch 1960), the birds are exceptional in having the highest reproductive potential of any Central American passerine so far studied (Skutch 1960). The clutches average three or four eggs in Central America, more than most other small tropical passerines (Skutch 1953, 1954, 1960). More striking is the HWs capacity for raising multiple broods during a breeding season that may extend over the entire year (Haverschmidt 1952, Skutch 1953, 1960, Alvarez-López et al. 1984, Freed, pers. comm., this study).

At Monteverde, HWs laid eggs from February through August (Fig. 2-1), and one pair raised a successful brood in October 1982. All clutches begun after June were second or third broods. Freed (pers. comm.) found a few nests in October and November of 1982, and Skutch (1953) found a nest in December. Haverschmidt (1952) collected eggs in every month of the year in Surinam. Egg-laying peaked during April at Monteverde, in lowland Costa Rica (Skutch 1953, 1960), and in lowland Panama (Freed, pers. comm.), just before the beginning of each rainy season. Egg-laying of Colombian HWs peaked in the wettest months there, in April and November/December (Alvarez-López et al. 1984).

Figure 2-1. Timing of breeding in four neotropical wrens. HW = House Wren, PW = Plain Wren, RW = Rufous-and-white Wren, GW = Gray-breasted Wood-Wren. The number of clutches initiated during each 1/2-month interval is shown by the histograms. Dashed lines above each histogram represent periods during which I observed wrens feeding nestlings, and solid lines represent periods during which I observed fledged young with their parents on natal territories.


GW
RW
PW
HW
10
5
0
25
20
15
J
F
M
A
M
J
J
A
S
O
N
D
NUMBER OF CLUTCHES INITIATED
ALL YEARS (1981–1983)

Fifty-eight percent of HW clutches at Monteverde contained three eggs and the rest contained four eggs; the average clutch size was significantly higher than any of the other wrens I studied (Table 2-1). The clutch size of individually marked females was invariable--that is, where I have information on the clutch size of marked females over more than one clutch (in some cases up to four clutches), any one female always laid the same number of eggs, either three or four. Mean clutch sizes at other tropical locations are similar, but two, five, and six egg clutches have been reported elsewhere (Skutch 1953, 1960, Alvarez-López et al. 1984, Freed, pers. comm.).

At Monteverde, pairs commonly raised two, and sometimes three, broods in a season. In the lowlands of Costa Rica and Panama, two, three, or four broods are reared each year (Skutch 1953, 1960, Freed pers. comm.). Skutch (1953) reported one pair that produced six clutches in one year, but only raised one brood successfully. Alvarez-López et al. (1984) reported one female that laid 14 eggs in five nests in one year; only one of these nests was successful.

The time from fledging or loss of one brood to the start of the next clutch ranged from 9 to 86 d (mean = 31 d, s = 16.7 d) at Monteverde. Re-nesting following loss of a nest usually occurred within 20 d, sooner than the start of a new nest following successful fledging. One pair, however, began a second clutch 9 d after successful fledging of the chicks in their first brood. Skutch (1953, 1960) reported an average of 24.5 d between fledging and re-nesting (range 14-36 d). Both Skutch (1953, 1960) and Freed (pers. comm.) found new clutches initiated before independence of a previous brood, that is, while the fledglings

Table 2-1. Life history traits of four wrens at Monteverde, Costa Rica.

	HW	PW	RW	GW
Number of months clutches initiated	8	5	4	3
Mean clutch size	3.4 (38)	3.0 (6)	2.9 (12)	2.0 (6)
Number of broods/yr	2-3	1[a]	1[a]	1
Days of incubation	13.7 (7)	14.0 (2)	15.3 (3)	$\geq$18 (2)
range, d	12-15	14	14-17	--
Nestling period, d	15.1 (15)	13.0 (1)	13.5 (2)	18-21 (1)
range, d	11-18	--	13-14	--
Combined incubation and nestling period	28.8	27.0	28.8	$\geq$36
Mean adult weight, g	13 (34)	18 (17)	27 (24)	17 (26)

Numbers in parentheses are sample sizes.
[a]Rarely two broods in a season.

were still on the natal territory. In the case reported by Skutch (1953), the older chicks became helpers at the nest of their younger siblings. I did not observe brood overlap at Monteverde.

Incubation and nestling times at Monteverde averaged 14 and 15 d, respectively (Table 2-1), and are in general agreement with similar values from Skutch (1960) and Alvarez-López et al. (1984). Parents brought food to their young for a few weeks after they left the nest. With three exceptions, all late nests initiated between June and August, I saw no chicks on natal territories after one month. I saw chicks from these three nests in the company of their parents on natal territories 2-3 months post-fledging (Fig. 2-1). Skutch (1960) noted that, although fledglings usually leave the natal territory within a few weeks of leaving the nest, the season's last brood may receive food from the parents up to five weeks later.

I observed three adult HWs, two banded parents and an unmarked wren known not to be an offspring of a previous brood, feed chicks at one nest in May 1982. An unmarked HW repeatedly came to the nest with food and succeeded in feeding the chicks sometimes but was usually driven from the nest by both parents, usually the male. The unmarked HW persisted in returning a minute or two later when the parents were away looking for food; it consistently approached the nest via concealed routes other than those used by the parents and, when the parents were not present, flew rapidly to the nestlings, fed them, and hurried away. The unmarked HW fed the nestlings for 5 d and then disappeared. I believe this is a case of misdirected parental care (e.g. see Price et al. 1983), rather than an example of cooperative breeding involving helpers at the nest.

Plain Wrens

PWs, although not as cosmopolitan as HWs, occur in a diversity of habitats from southern Chiapas, Mexico, to central Panama (Peters 1931: 412; A.O.U. 1983). In Costa Rica, they range from sea level to highlands at about 2200 m and are especially widespread on the Pacific slope (Carriker 1910: 756, Peters 1931: 412, Slud 1964: 285, Arnold 1966). PWs are found primarily in open or semi-open areas overgrown with shrub thickets and tangled foliage, but also range into humid forest undergrowth, mangroves and canebrakes in Tropical and Subtropical zones (Skutch 1960: 134, Slud 1964: 285, A.O.U. 1983). At Monteverde PWs are common in regenerating fields and gardens near dwellings, and along roadsides to the upper extent of agricultural clearings at about 1500 m. PWs typically remain in low undergrowth of secondary vegetation and rarely venture into the large open areas frequented by HWs; nor did I see them in forest interior at Monteverde. Thus, the habitat of PWs lies between and overlaps both the habitats of HWs and of RWs.

I found six active PW nests at Monteverde. The nest sites and construction were similar to those described by Skutch (1960: 134). All were less than 1.5 m high and built in a bush, a tangle of vines, or a grass clump low over the ground. The nests were globular with a side entrance angled down and covered by a short extention of the roof. Nests were loosely constructed of grass blades and strips of leaves, with a softer lining of the same material and plant fibrils (construction corresponds to Skutch 1960: 135, Fig. 21a).

At Monteverde, nests were initiated between March and July (Fig. 2-1) and all of them contained three eggs (Table 2-1). Skutch (1960)

found active nests in Costa Rica from January to August/September, and Arnold (1966) estimated a peak in breeding activity in Costa Rica from June to August based on examination of gonads and presence of juveniles in museum collections. Seven of nine nests found by Skutch (1960) contained only two eggs; he found one nest each with one and three eggs. Skutch (1960) measured an incubation time of 18 d at one nest, somewhat longer than the 14 d interval I measured (Table 2-1). Nestling periods measured at each site were the same, 13 d.

I found one case of re-nesting in Plain Wrens. A single chick fledged in mid-May 1982 from a nest also containing two infertile eggs. The same pair initiated a second clutch in late July that produced three young. All four young of the year remained on the natal territory until September 1982. In general, PW fledglings remained on the natal territory about one month, but the first fledgling described above stayed with its parents for six months (Fig. 2-1).

Rufous-and-white Wrens

RWs range from Chiapas, Mexico south to western Panama; this and a similar form, Thryothorus nicefori may constitute a superspecies; the range of the latter continues south into Colombia and northern Venezuela (Carriker 1910: 757; Peters 1931: 411; A.O.U. 1983). Although RWs occur locally on the Caribbean slope in parts of their range, they are restricted to the Pacific slope in Costa Rica, and may be found either in relatively open, dry woodlands or in wetter forest up to about 1500 m in the Cordillera de Tilarán (Slud 1964: 285; Arnold 1966). At Monteverde, RWs inhabit dense second growth woodland regenerating in tracts between farms below 1500 m. They also frequent the edges and tangled thickets adjoining these woods.

Two nests recorded by Carriker (1910: 757) were 3 m high in forks of small trees. Arnold (1966) found three elbow-shaped nests, all about 2 m high, and noted that each had some form of natural protection: one was adjacent to an active wasp nest; one was in a spiny palm (Bactris spp.) and one in Acacia spp. All of the nests I found in Monteverde were from 2-4 m high and draped over branches at the center of small trees. Trees with thorns and spines were preferred. I found 25 inactive nests and three-fourths of these were in spiny palms; the rest were in exotic trees with thorns or spines. Of the 14 active nests I found, eight were in spiny palms (one of these was also on top of an active wasp nest and one hung over a stream); four nests were on thorny exotic trees, and the remaining two were draped over the outer branches of an Inga spp. tree overhanging a bank. The large, covered nests were constructed of tightly woven twigs and fibrils. The front entrances were elongated into tunnels equal in length to the nest chambers at the rear, but narrower (Skutch 1960: 135, Fig. 21b).

Of the four species at Monteverde, the nest sites selected by RWs were the most specialized. RWs appeared to select nest sites where the nests would be inaccessible to predators. Nest site selection in relation to predation, particularly regarding avian-hymenopteran nesting associations, has been studied by Janzen (1969), Smith (1980), Wunderle and Pollock (1984) and F. Joyce (unpubl. data).

RW clutches at Monteverde were initiated between April and July; Carriker's (1910) two nests were collected in May and June and Arnold (1966) found active nests in July and August. Clutch sizes at 12 Monteverde nests ranged from two to four (Table 2-1); most nests had three eggs. The two nests recorded by Carriker (1910: 757) each

contained four eggs; one nest from Panama also contained four eggs (Morton and Farabaugh 1979). Arnold (1966) found one nest with three chicks. Incubation and nestling periods were similar to those of HWs and PWs with a combined length of about 29 d (Table 2-1). I observed three cases of re-nesting in a single breeding season. In the first, a pair began a second clutch on 3 June 1982 after chicks from their first nest died in late April. In the second case, a new clutch was completed on 22 June 1982 after chicks in the first nest died on 29 May. And in the third case, a pair successfully raised two broods; chicks from the first nest fledged in late April and a second clutch was laid in early June. In all three cases, 4-6 weeks elapsed between active nests. I saw young RWs on their natal territory for 1-2 months post-fledging (Fig. 2-1).

Gray-breasted Wood-Wrens

GWs inhabit the dense undergrowth and tangled thickets of humid montane forest, edges and dense secondary growth from the highlands of Mexico south through Colombia and northern Venezuela, west of the Andes to western Ecuador and east of the Andes to eastern Peru and northern Bolivia (Carriker 1910: 761, Peters 1931: 432-435, A.O.U. 1983). At Monteverde, GWs are among the most common understory birds in the cloud forest; they are less common at the lower extent of their range, from about 1350 - 1400 m. Some GWs share lower second growth woods with RWs, and more recently with White-breasted Wood-Wrens.

All active nests I found, and several recorded by Skutch (1960), were compact globular structures (Skutch 1960: 135, Fig. 21d) placed 1-2 m high in the spreading upper branches of understory saplings or shrubs, usually overhanging a bank, ravine, trail or stream. The nests were

constructed of moss, fibrils, and rootlets, and partly covered by foliage; thus, they were quite cryptic to me, as globular masses of moss and plant fibrils are suspended in vegetation virtually everywhere in the cloud forest.

Clutch initiation in GWs occurred in fewer months than in the other three wrens. All 14 clutches I found, and all egg sets reported by Carriker (1910:762) and Skutch (1960) were initiated from March to May (Fig. 2-1). Six nests at Monteverde (Table 2-1), three nests found by Skutch (1960), and two reported in Carriker (1910: 762), all contained two eggs. I could not ascertain the incubation and nestling periods precisely, but they were longer than in the other three wrens. Two GW nests at Monteverde required at least 18 d of incubation to hatch (Table 2-1), and one nest followed by Skutch (1960) hatched after 19 or 20 d. I recorded a nestling period of 18-21 d at one nest, and Skutch (1960) recorded 17-18 d at one nest. The incubation and nestling cycle for GWs is at least 7 d longer than those of the other three species I studied. I did not observe re-nesting in GWs either following loss of a nest or successful fledging. Young GWs stayed on their parent's territory for 5-6 months (Fig. 2-1). Three times, twice in late July, and once in October, I saw GWs and their offspring construct a nest together. These nests were probably used for sleeping (e.g. Skutch 1960). Young GWs apparently dispersed before the following breeding season; I never saw more than two GWs on a territory containing an active nest.

Predation at Wren Nests

I measured far greater nesting success at HW nests than for any other wrens. Seventy-three percent of all HW eggs produced fledglings, whereas less than half of the eggs produced by other species survived to

fledging (Table 2-2). RWs and GWs, the two forest wrens, suffered the greatest mortality at nests. Predation was least frequent at HW nests, accounting for the loss of only 12% of the offspring, and most common at GW nests in cloud forest.

Other biologists have reported lower predation rates among birds nesting in open habitats near human dwellings, as compared with birds nesting in forest (Snow and Snow 1963, Skutch 1966, 1967, 1985, Ricklefs 1969). In addition, Wesolowski (1983) found a lower incidence of nest predation among Wrens (Troglodytes troglodytes) under secondary conditions, as compared with Wrens in primeval forest. In contrast, Oniki (1979) reported higher predation at nests in open areas, but her open study sites in Brazil were not inhabited by people, and much of the predation in open habitats was due to ants. Ants were not significant predators in any other studies. Several authors have suggested that predation rates may be lowered in open habitats because man's activities there reduced the number of nest predators (Skutch 1966, 1967, Loiselle and Hoppes 1983, Wilcove 1985). In order to test the hypothesis that man's activities reduced predation at wren nests, I compared predation rates at HW nests on and off active buildings at Monteverde (Table 2-3). Egg predation was rare in both groups, but 23.5% of the chicks in nests away from buildings were lost to predators, whereas none of the chicks on buildings was preyed upon. Nests not on buildings were clearly more vulnerable during the chick stage while parents making frequent trips to nests would have been conspicuous.

Some eggs of all species were infertile. Ten HW eggs were destroyed when nests flooded or caved in and three RW eggs were lost when a nest blew down. Sources of chick mortality other than predation

Table 2-2. Nesting success and predation at Monteverde wren nests.

	Nests (n)	Eggs (n)	% Eggs hatch	% Eggs fledge	% Eggs pred.	% Chicks pred.	Total % pred.
HW	38	130	78	73	8	5	12
PW	5	15	67	47	20	30	40
RW	11	32	78	31	9	24	28
GW	6	12	50	33	33	33	50

Table 2-3. Nesting success and predation at House Wren nests on and off of buildings.

	nests on buildings	other nests
number of nests (n)	21	17
number of eggs (n)	73	57
% eggs preyed upon	6	7
% chicks preyed upon	0	24
% total offspring preyed upon	6	21

were as follows: two HW chicks left their nest prematurely following human disturbance and subsequently died, two RW chicks were deserted, and seven RW chicks from two nests died during May 1982 when Monteverde received over 600 mm of rain. Three of the latter also were heavily infested with subcutaneous fly larvae (F. Muscidae; botflies). I found only one other brood of wrens infested with botflies at a HW nest. Although the four chicks in this brood were infested with more than 12 larvae each, they fledged at a normal age and weight.

Discussion

The four species included in my study represent a wide range in habitat preferences and reproductive output even though they belong to the same family and are found sympatrically. At one extreme, HWs have the greatest range, both geographically and with respect to the diversity of habitats they occupy. HWs inhabitat areas that have undergone the greatest alteration by man, and may select nest sites close to man's activities because there is less danger of nest predation there. Although the clutch sizes of HWs at Monteverde are not very different from those of other wrens there, they were the only wrens to commonly raise two or three broods in a single breeding season that spanned large portions of both wet and dry seasons. From the most open habitats at lower elevations through regenerating woods and up into wet cloud forest, wren species show a decrease in clutch size, a constriction of the breeding season, and, in GWs, a marked increase in the length of the nesting cycle and period of parental care.

An extensive literature deals with the complex interplay between demography and the environment (see reviews by Stearns 1976, 1977, Southwood 1977, Horn 1978, Parsons 1983). Two current models pertinent

to birds predict combinations of life history traits relative to environmental patterns (Parsons 1983). The deterministic model (r-K selection), based primarily on the ideas of Dobzhansky (1950), MacArthur and Wilson (1967) and Pianka (1970, 1972), assumes non-fluctuating mortality and fecundity schedules (Stearns 1976). It predicts smaller reproductive effort, fewer offspring, and later maturity in stable resource-limited environments that favor competitive ability and predator avoidance, because populations are at or near carrying capacity. Earlier maturity, larger reproductive effort and more offspring are predicted in fluctuating environments that favor rapid population growth in response to frequent episodes of recolonization. These two situations are generally considered to represent the extremes of an environmental continuum roughly corresponding to early successional (r-selected) and late successional (K-selected) environments (Southwood 1977).

The stochastic (bet-hedging) model, based on the work of Murphy (1968) and Schaffer (1974), deals directly with the effect of environmental fluctuations on adult and juvenile mortality (Stearns 1976). This model predicts a combination of traits similar to that predicted by the deterministic model when the fluctuating environment is one that results in variable adult mortality. That is, when adult survival is uncertain, organisms should expend a large amount of reproductive effort early in life. On the other hand, the bet-hedging model predicts that a fluctuating environment resulting in variable juvenile mortality favors later maturity, reduced reproductive effort, and fewer young spread out over a longer period, so that the risk of

total reproductive failure is minimized. This tactic is the opposite of that predicted for a fluctuating environment by the r-K selection model.

These models are not mutually exclusive; evidence from birds implicates the interplay of population density relative to resources (emphasized by the r-K selection model) and the direct influence of environmental fluctuations on mortality patterns (emphasized by the bet-hedging model) in the evolution of reproductive tactics. For example, Cody (1966, 1971) suggested that the trend for latitudinal decline in clutch size may reflect a general trend in reduced reproductive commitment with increasing environmental stability. Based on a hypothesis originally proposed by Ashmole (1963), Ricklefs (1977, 1980) later suggested that density-dependent mortality during the non-breeding season influences reproductive rate by limiting population size during the breeding season. Ricklefs (1980) suggested that variation in the seasonality of resources is the single most important factor causing geographical patterns in clutch size, since seasonality directly determines fluctuations in population density. Similar reproductive patterns over smaller geographic differences lend support to this hypothesis. Birds in open, more seasonal habitats typically produce larger clutches and more broods per season than relatives in adjacent forests (Snow and Snow 1963 for Turdus thrushes in Trinidad, Lack and Moreau 1965 and Lack 1968 for tropical regions, Brewer and Swander 1977 for eastern North America). Wrens of temperate grassland and marsh have higher reproductive output than wrens in more forested habitat (Welter 1935, Kale 1965, Verner 1965, Brewer and Swander 1977).

In addition to the lower reproductive effort in GWs, higher predation rates at the nests of forest wrens resulted in low

reproductive success. I estimated the average reproductive output of wrens by multiplying the average clutch size times the average number of broods/yr times the percent of offspring surviving to fledging. I estimated reproductive output of HWs using 2 broods/yr. HWs averaged 5 fledglings/yr as compared with 1.4, 0.9 and 0.7 fledglings/yr for PWs, RWs and GWs, respectively. HWs achieved the greatest reproductive output through a combination of slightly larger clutches, greater nesting success and multiple brooding. Using only one brood/yr to estimate HW reproductive output yields 2.5 fledglings/yr, still significantly more than the other species. Apparently, the capacity of other wrens to raise more than one brood in a season is restricted by factors that do not affect HWs or are somehow circumvented by HWs. For GWs, the potential to re-nest must be influenced by the length of family ties. Presumably, it is more beneficial to the parents if the young remained on the natal territory, than if the parents began another clutch. Juvenile survival may be enhanced while the young remain dependent on the parents and their territory, through protection from predators and/or because juveniles benefit by learning techniques for catching prey (Norton-Griffiths 1969, Dunn 1972, Fogden 1972, Davies 1976, Morse 1980). In contrast, the benefits to young HWs staying on natal territories must be low in comparison to the benefits their parents stand to gain by raising more broods. If predation rates are low and food is abundant, then the expected success of raising more than one brood is high.

What characteristics of HWs and/or their habitats enable them to exploit open, disturbed habitats and maintain a higher reproductive potential than most other Central American passerines, including

sympatric PWs that share similar, but not identical habitats? My data suggest that, as a result of their selection of nest sites near man, HWs avoid predation of their chicks. Two other factors contributed to the high HW reproductive rate: larger clutches and multiple brooding in an extended breeding season. Several authors have suggested that high predation rates at nests may act as a selective pressure for lower clutch size (Skutch 1949, 1967, Ricklefs 1970, Cody 1971, Perrins 1977, Slagsvold 1982, 1984); thus, larger clutch size might result from lower predation rates in HW habitats. Alternatively, or in additon, larger clutches can result from greater food abundance (Anderson 1977, Hogstedt 1980, Swanberg 1981, Village 1981, Findlay and Cooke 1983, Marr and Raitt 1983). The third factor, a long breeding season, also depends on higher food availability for a greater part of the year than for species that have a shorter breeding season. In subsequent chapters I investigate, first, the environmental potential for maintaining high reproductive rates, and second, the behavioral capacity of different wrens to exploit this potential through foraging flexibility.

CHAPTER III

VARIABILITY IN THE ARTHROPOD FOOD SUPPLY

To investigate my initial hypothesis that the open, disturbed habitats occupied by HWs and PWs should have the most variable food supply, I monitored food supplies in six wren habitats. I gathered data to answer the following questions: In what habitats does the food supply vary more? What aspects of the food supply determine this variability? What habitats offer the best potential for a high reproductive output? What aspects of the food supply determine this potential? I estimated variation in the food supply among different habitats by comparing temporal (seasonal) and spatial (over different patches within a habitat) variability in five parameters that may determine prey availability: abundance, biomass, composition, dispersion, and use of substrates.

Methods

Habitats

I distinguished six habitat types within the Monteverde study area (Fig. 1-1). From the most open, disturbed habitats to the least disturbed forests these were as follows:

1. Pastures: tracts cleared for grazing dairy cattle; at Monteverde, pastures contained scattered large trees, decaying logs, and a few small shrubs. They were bordered by remnant tracts of woods (Habitat 5 below).

2. Early successional shrub: overgrown clearings and gardens that contained banana trees and other small, cultivated trees (coffee and citrus) with a dense underlying layer of tangled shrubs, vines, grass and herbaceous foliage from 0.5 to 2 m high.

3. Woodland edges: borders of moist woodlands below 1500 m. Edges typically consisted of low, dense herbaceous foliage, shrubs and saplings up to 2 m high, and taller layers of forest understory and trees (see Habitat 5 for dominant plant families).

4. Cloud forest gaps: edges and interiors of natural treefall gaps and man-made cutovers along a rugged dirt road that bisected the Preserve. All of the gaps were within wet cloud forest above 1500 m. Typically, gaps had a very tangled layer of fallen trees and epiphytes overgrown by dense layers of successional plants (especially Acanthaceae, Rubiaceae, Solanaceae and Heliconia spp.) up to 2 m high.

5. Lower elevation woods: tracts of moist forest below 1500 m that remained between clearings. The canopy averaged about 10 m high with the most dominant trees belonging to the families Lauraceae and Ficaceae. The understory, although having a less dense foliage than in wetter cloud forest (Habitat 6), was usually cluttered with tangled woody vines and plants most commonly in the families Rubiaceae, Melostomaceae and Palmaceae.

6. Cloud forest: the interior of wet montane forest above 1500 m. The forests, dominated by Lauraceae and Melicaceae, supported a dense epiphytic growth and a dense, leafy understory dominated by plants in the Rubiaceae.

Sampling Periods

I sampled arthropods during 17 sample periods from September 1981 through July 1983. I sampled between 0900 and 1400 hrs on 8-9 d every 4-8 weeks, choosing days having as similar weather conditions as possible. I scrambled the order in which sites were sampled during each sample period to minimize bias due to weather differences within and between days. The midpoint dates of sample periods were 23 September, 1 November, 1 December, and 30 December 1981, 12 February, 22 March, 28 April, 21 June, 20 July, 25 August, 27 September, and 28 November 1982, 25 January, 16 March, 27 April, 9 June, and 14 July 1983.

From September 1981 - August 1982 I sampled four sites in each of the six habitats, and from September 1982 - July 1983 this was reduced to three sites within each habitat (Fig. 1-1). Four adjacent transects were sampled within each site.

Sampling Procedure--Visual Sampling

I used a visual sampling technique to estimate the relative differences in arthropod populations among the six habitat types. Each sample unit, or transect, consisted of a thorough, seven-minute search for any arthropods on all substrates between 0-2 m high and within an interval 1 m wide. Transects varied from 10-30 m in length, depending on vegetational density at the site. I carried a stopwatch to accumulate search time but did not include the time to record entries. I searched all exposed surfaces (e.g. leaf tops, twigs, tree-trunks) and also the undersides of leaves and stems, leaf bracts, shallow holes and crevices in woody surfaces, and inside rolled leaves and aerial leaf litter. I did not search the interiors of dead logs, crevices deeper than 10 cm or under ground litter, but I did count animals on the

surface of ground litter. I standardized transects by search time rather than search area for two reasons: 1) First, great differences in vegetational density among different habitats would have required that far greater periods of time be spent searching the same area in some habitats than in others. 2) For a generalist insectivore, therefore, I thought relative time spent searching for food was a better estimate of food availability than area searched.

My visual sampling technique was biased in favor of inclusion of large, conspicuous prey, but I chose it because I thought that a careful search of substrates, in imitation of generalist foliage-gleaning wrens, was a more suitable technique to estimate food availability for visually-oriented birds than other conventional techniques (e.g. sweep-sampling, sticky traps, and suction traps). Sweep-sampling is widely used, but was not appropriate for comparative studies in the different habitats that occurred at my site because of the vast differences in vegetation density among different habitats (Southwood 1978). I found sticky traps to be highly biased in favor of small flying insects (unpublished data; see also Southwood 1978), as are Malaise traps (Buskirk and Buskirk 1976). In addition, certain advantages of the visual technique rendered it most suitable for my study. Visual sampling allowed me to sample surfaces not included by other methods but important to wrens (e.g. woody crevices, leaf bracts, etc.); and visual sampling enabled me to record arthropod clumps, prey substrates and apparent crypticity, important determinants of prey availability that are not sampled by other methods.

I counted and recorded information for each individual arthropod except superabundant Diptera and Homoptera in the smallest size category

($\leq$ 5 mm long; see below); I estimated numbers of flies and hoppers at 30-second intervals during the seven-minute search. For each animal I recorded the following information:

1. Type: I identified arthropods to order. I made no attempt to identify species since arthropods were usually not collected. Arthropod groups were 1) Arachnida, 2) adult Lepidoptera, 3) larvae (97.6% lepidopteran larvae, 1.9% coleopteran larvae, and 0.5% other larval forms4) Diptera, 5) flying Hymenoptera (wasps and bees), 6) ants, 7) Homoptera, 8) Hemiptera, 9) Orthoptera, 10) Coleoptera, and 11) other groups and unidentified arthropods. The preceding category numbers appear in the following text and figures.

2. Size length class: I estimated the length of each individual using a 10 cm ruler. These were 1) $\leq$ 5 mm, 2) 6-10 mm, 3) 11-20 mm, 4) 21-35 mm, 5) 36-55 mm, and 6) $\geq$ 56 mm.

3. Substrate: I distinguished 24 categories in the field, but lumped these into 10 for data analysis as follows: 1) air (flying or suspended on thin silk), 2) exposed foliage (e.g. leaf tops), 3) foliage undersides and stems, 4) concealed foliage (bracts, rolled leaves), 5) concealed in aerial leaf litter, 6) grass and near-ground herbaceous foliage, 7) ground litter, 8) twigs and branches less than 5 cm in diameter, 9) wood surfaces (logs, limbs, stumps and tree trunks greater than 5 cm in diameter), and 10) woody crevices (holes and crevices in logs and trees, and under loose bark). I defined categories 3, 4, 5 and 10 as concealed substrates for data analysis (see Results); all other categories are exposed substrates.

4. Cryptic: I recorded whether or not the animal appeared cryptic to me on the substrate where I found it.

5. Clumps: I counted arthropods in clumps as separate individuals, but I recorded the size of each monospecific clump. Clumps of more than one species were so infrequent as to be of negligible importance and I did not include those in the clump analysis. I defined a clump as three or more individuals within 2 cm of each other, or, in the case of social Hymenoptera, I included individuals from the same colony.

6. Biomass: I used the relationship described by Rogers et al. (1976) to estimate biomass represented by each arthropod group on a given transect, for each sample period,

$$W = 0.0305\ L^{2.62}$$

where W = dry weight in mg
and L = length in mm (I used the midpoint of each size length class for L).

In addition, I coded data by sample period, date, habitat type, site number, transect number, precipitation, wind speed, temperature, cloud cover, and time of day.

I transcribed data to personal computer files and performed statistical analyses with BASIC statistics programs (specific analyses are described in Results, below). I tested for differences in variances and coefficients of variation (CVs) using the Miller Jacknife technique (Van Valen 1978).

Total abundance measures were greatly influenced by the large numbers of tiny Diptera and Homoptera, especially in open habitats. In all analyses of abundance, I have omitted animals in Size Class 1 ($\leq$ 5 mm). Because biomass estimates include, but de-emphasize, these tiny arthropods, I performed most analyses of food availability using biomass, rather than abundance.

Results

Arthropod Biomass and Abundance

Temporal variation in arthropod biomass and abundance

Biomass and abundance of arthropods were much higher in open habitats than in the two forest habitats. The greatest prey numbers that I found in forest habitats only barely overlap the lowest numbers sampled in open habitats (Figs. 3-1, 3-2). Prey biomass and abundance in woods edges and cloud forest gaps was usually intermediate between that of adjacent open and forest habitats and was comprised of taxa from both adjacent open and forest habitats.

In the two most open habitats, pastures and early successional shrub, numbers generally peaked during the late dry season-early wet season transition periods (March-July), but distinct seasonal patterns were absent; numbers and biomass remained high all year, with little regularity in the timing of fluctuations (Figs. 3-1, 3-2).

In contrast, clear seasonal peaks were evident in low elevation woods during the rainy seasons (July-November) of 1981 and 1982. Unseasonal rains in March 1983 were followed by an extraordinarily dry wet season (this was an El Niño year) and were correlated with an earlier, smaller peak in arthropod numbers in woods (Figs. 3-1, 3-2).

Seasonal changes in woodland edges resembled the temporal patterns of adjacent woods more than those of open habitat, but peaks in the dry season (Feb/March 1982) reflected increases in prey from adjacent open areas. Biomass and numbers in woods and edges decreased with the onset of the dry season each year (Figs. 3-1, 3-2).

Similarly, biomass and numbers in cloud forest were lowest during the early dry season, increased during the late dry season, and peaked

Figure 3-1. Temporal changes in arthropod biomass in six Monteverde habitats, 1981 - 1983. Letters on the horizontal axis refer to months of the year.

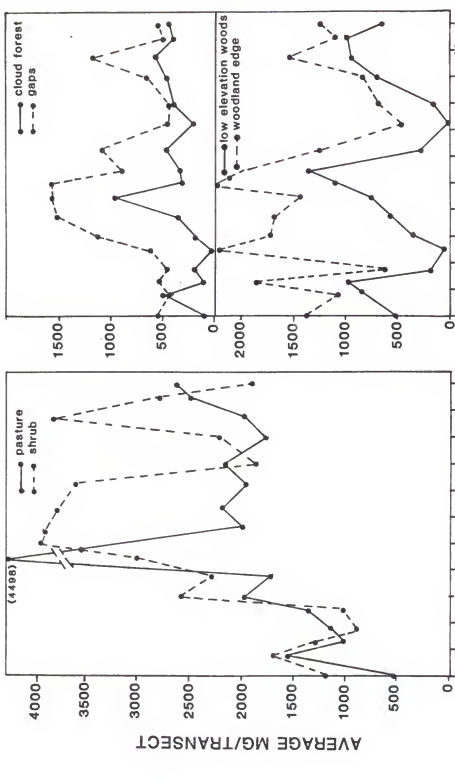

AVERAGE MG/TRANSECT
(4488)
pasture
shrub
cloud forest
gaps
low elevation woods
woodland edge
S N J M M J S N J M M J
1981 1982 1983
0 500 1000 1500 2000 2500 3000 3500 4000

Figure 3-2. Temporal changes in numbers of arthropods (greater than 5 mm in length) in six Monteverde habitats. Letters on the horizontal axis refer to months of the year.

AVERAGE NUMBER OF ARTHROPODS/TRANSECT
pasture
shrub
cloud forest
gaps
low elevation woods
woodland edge
0
50
100
150
20
40
60
80
S N J M M J S N J M M J
1981
1982
1983

with the onset of each rainy season (April-June). Unlike the pattern in woods at lower elevations however, prey numbers peaked earlier in the wet season in cloud forest (July-August vs. September-November). Again, the early peak in 1983 reflects unseasonal March rains. Seasonal patterns in prey availability were similar in cloud forest gaps, but biomass and abundance were much higher in light gaps than in adjacent cloud forest (Figs. 3-1, 3-2).

Marked fluctuations in biomass and abundance occurred in all habitats, but in the forest habitats, where prey availability was generally much lower, relative temporal fluctuations were the most severe. The coefficients of variation (CV = s/n x 100) for temporal changes in biomass and abundance were greatest in the two forest habitats (Table 3-1). Variances associated with both measures were significantly greater in forests and woods (Miller Jacknife; F(biomass) = 4.78, df = 5,96; $P<0.01$; F(abundance) = 4.83, df = 5,96, $P<0.001$), and the CVs in abundance were significantly greater in forests and woods as well (Miller jacknife; F(abundance) = 2.53, df = 5,96; $P<0.05$).

In addition, I calculated the percent change (either positive or negative) in biomass, and in abundance, from each sample period to the next one. Percent changes in prey availability averaged much higher in the two forest habitats than in more open habitats (Table 3-2). These results are consistent with those estimating temporal variation by the CV; both suggest that temporal variation in biomass and in abundance were greater in forest habitats than in more open habitats.

Table 3-1. Temporal variation in biomass and abundance of arthropods in six Monteverde habitats.

Habitat	CV in Biomass (n = 17 periods)	CV in Abundance[a] (n = 17 periods)
Pasture	46 %	43 %
Early successional shrub	44	38
Low elevation woodland edge	42	43
Cloud forest gaps	50	58
Low elevation woods	58	82
Cloud forest	61	75

[a]Abundance of arthropods greater than 5 mm in length.

Table 3-2. The average percent change, over consecutive sample periods, in biomass and in numbers of arthropods in six Monteverde habitats.

Habitat	% Change in Biomass (mean over 16 intervals)	% Change in Abundance[a] (mean over 16 intervals)
Pasture	41	50
Early successional shrub	34	41
Low elevation woodland edge	54	47
Cloud forest gaps	33	64
Low elevation woods	94	82
Cloud forest	104	69

[a]Abundance of arthropods greater than 5 mm in length.

Spatial variation in biomass

I estimated spatial variation in prey availability in two ways: through inter-transect variability in arthropod biomass, and through the occurrence of arthropod clumps.

Inter-transect variability in biomass. I determined the CV in biomass among the four transects at each site and pooled each of these values for all sites and all sample periods within each habitat. The mean CV for the pooled values estimates differences in prey biomass over adjacent transects within a habitat and is significantly greater in the two forest habitats and in cloud forest gaps, than in low elevation open and edge habitats (Table 3-3; parametric ANOVA, $F = 6.06$, $df = 5.36$, $P<0.001$). Thus, at a given time of the year, adjacent patches of forest and gap habitat had greater variance in prey biomass than did adjacent patches of more open, drier habitat.

To determine if there was a seasonal component to the degree of inter-transect variation in biomass I ranked sample periods within each habitat from the lowest to the highest CV for inter-transect biomass (Table A-1, Appendix) and performed a Kendall test for concordance (Siegel 1956). The ranks for different habitats were significantly related ($X^2 = 29.20$, $df = 16$, $P<0.02$); thus, inter-transect variability had a seasonal component that was consistent across all habitats. During periods of extreme weather CVs tended to be high in all habitats; thus, the spatial distribution of prey biomass was most patchy during those times 1) when rainfall exceeded 500 mm in October 1981, 2) late in an unusually dry season March-April 1982, and 3) during November 1982 when insects were sampled during a dry spell following a very wet rainy season.

Table 3-3. Variation in biomass of arthropods among transects within habitats.

Habitat	Number of site-periods	Mean CV in biomass over four transects	standard deviation (s)
Pasture	61	52.4	30.6
Successional shrub	61	53.9	21.7
Woodland edge	61	65.4	32.3
Cloud forest gaps	59	75.0	34.0
Low elevation woods	61	76.6	38.1
Cloud forest	60	70.8	39.1

Spatial distribution of arthropods--the occurrence of clumps.

Over half of the individuals I found in clumps were harvestmen (Class Arachnida, Order Phalangida), but because these were relatively small animals (0.4-1 cm body length), they contributed only 20% of the biomass in clumps (Table 3-4). Adult Coleoptera (especially of the families Chyrsomelidae, Curculionidae, and Cerambycidae), Hemiptera, and larvae also comprised significant portions of the biomass that occurred in clumps. The seasonality and distribution of clumps was therefore dependent on the seasonality and habitat preferences of these four groups (Figs. 3-3, 3-4). During the late wet season (November) when numbers of harvestmen peaked, I found the greatest number of clumps in low elevation woods and edges. A seasonal peak in lepidopteran larvae during the same time contributed to peaks in clumping on woodland edges (Figs. 3-3, 3-4). During the wet season, over 50% of the total biomass in low elevation woods occurred in clumps. The percent of the total number of arthropods that were found in clumps averaged significantly greater in woods and edges than in other habitats (Kruskal-Wallis $H = 19.92$ $df = 5$, $P < 0.05$).

In habitats where harvestmen were rare, clumps were relatively uncommon and comprised various taxa (Fig. 3-4). In wet cloud forest and gaps, only lepidopteran larvae were predictably seasonal (dry-wet season transition peaks in clumping in gaps March-June of both years; Fig. 3-3). Other apparent peaks in clumping were the result of unique encounters with large clumps at one location on one day; e.g. the October 1981 peak in cloud forest resulted when I sampled a roost of over 100 large geometrid moths on one tree; hence the large biomass in

Table 3-4. The composition of arthropod clumps for all habitats and sample periods combined.

Arthropod Group	% of Clumped Individuals	% of Biomass in Clumps
Arachnida	52.9	20.0
Adult Lepidoptera	0.2	1.8
Flying Hymenoptera	2.3	7.0
Ants	5.8	3.8
Hemiptera	18.4	13.8
Adult Coleoptera	13.8	31.3
All Larvae	4.6	19.3
All Other Groups	2.0	3.0

Figure 3-3. Seasonal occurrence of arthropod clumps in six habitat types at Monteverde, 1981 - 1983. Letters on the horizontal axis refer to months of the year.

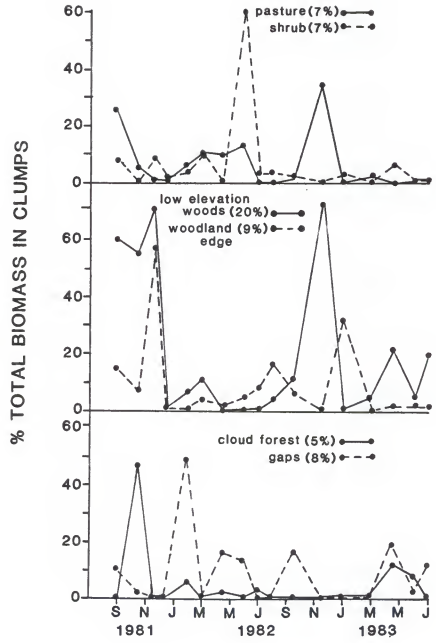
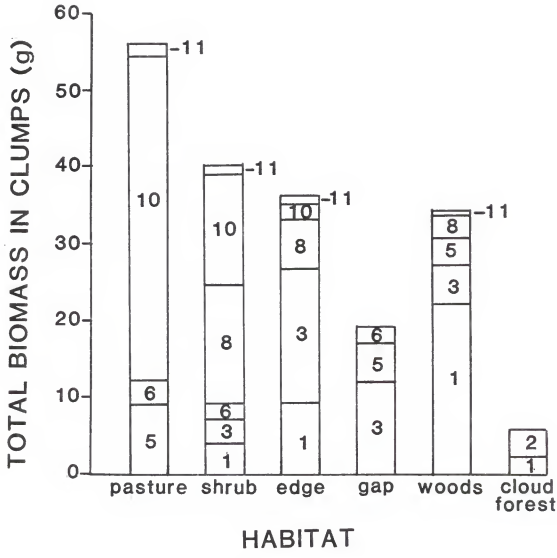

% TOTAL BIOMASS IN CLUMPS
pasture (7%)
shrub (7%)
low elevation
woods (20%)
woodland (9%)
edge
cloud forest (5%)
gaps (8%)
60
40
20
0
S
N
J
M
M
J
S
N
J
M
M
J
1981
1982
1983

Figure 3-4. Composition, by weight, of arthropod clumps in six Monteverde habitats. Numbers on histograms correspond to arthropod groups listed in Chapter Three, Methods: 1) Arachnida, 2) adult Lepidoptera, 3) larvae, 4) Diptera, 5) flying Hymenoptera, 6) ants, 7) Homoptera, 8) Hemiptera, 9) Orthoptera, 10) Coleoptera, 11) all groups that each had < 1% of the total.


TOTAL BIOMASS IN CLUMPS (g)
60
50
40
30
20
10
0
-11
10
6
5
-11
10
8
6
3
1
-11
10
8
3
1
6
5
3
-11
8
5
3
1
2
1
pasture
shrub
edge
gap
woods
cloud forest
HABITAT

one clump. Similarly, my encounter with a large wasp colony in a single gap in February 1982 resulted in a peak in clumping (Fig. 3-3).

Likewise, I could not associate occasional peaks in the occurrence of clumps in the two open habitats with the seasonality of any particular arthropod taxa. The peaks were the result of unique samples. In June 1982, 60% of the total biomass in pastures was from several clumps of chrysomelid beetles in a single pasture on one day. The peak in November 1982 in shrub habitat resulted from several small clumps of very large cerambycid beetles at one site on one day. Unlike the predictably high occurrence of clumps in lower elevation woods, the occurrence of clumps in open habitats, and in cloud forest and gaps, was less predictable over time, comprised a much smaller percentage of the total biomass (less than 10% in most months), and was not dependent on any particular taxa.

To compare variation in the distribution of clumps over different transects within a habitat, I calculated the proportion of all transects that contained at least one clump of arthropods. I averaged these proportions over all sites and sample periods to obtain an average proportion of transects containing at least one clump. In general, a higher proportion of transects in the more open, lower elevation habitats contained clumps (Table 3-5; Kruskal-Wallis $H = 37.53$, $df = 5$, $P < 0.01$). Whereas the variance (over time) in the proportion of transects with clumps did not differ significantly among habitats (Miller Jacknife test; $F = 1.92$, $df = 5,96$, $P>0.05$), the coefficient of variation in this proportion was significantly higher in cloud forest, gaps and woods ($F = 5.46$, $df = 5,96$, $P<0.001$). Thus, finding a clump on any given transect was most likely, and this probability stayed most

Table 3-5. The proportion of transects in each habitat containing at least one arthropod clump.

Habitat	% Transects with at least one clump	Standard Deviation	CV (%) (n = 17 periods)
Pasture	37.4	10.68	29
Successional shrub	37.4	20.39	54
Woodland edge	27.0	15.43	57
Cloud forest gaps	10.8	8.06	75
Low elevation woods	30.2	21.80	72
Cloud forest	12.5	16.86	135

constant over time, in pastures, and to a lesser extent, in early successional shrub and edges. Although predictable small clumps were spread uniformly throughout these habitats, the taxa they included (chrysomelid beetles in pastures, aposematic hemipterans in shrub, and ants and wasps in both) were not among the most important prey for wrens (see Chapter IV). In contrast, the proportion of transects containing clumps in low elevation woods was quite variable; during the wet season nearly half of the transects contained clumps of harvestmen or larvae that included over half of the total biomass sampled, but during the dry season, I found clumps on fewer than 10% of the transects. The occurrence of clumps in woods was predictable in time but unpredictable in space because the prey were dispersed and highly mobile. In cloud forest and gaps, the proportion of transects with clumps also varied a great deal over time, but the averages were very low (Table 3-5).

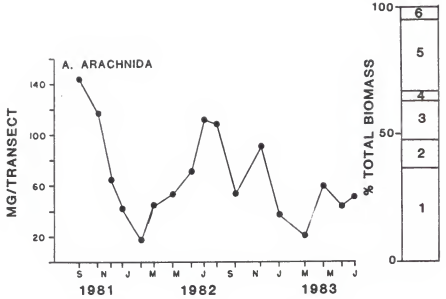
Spatial and Temporal Variation in Arthropod Composition

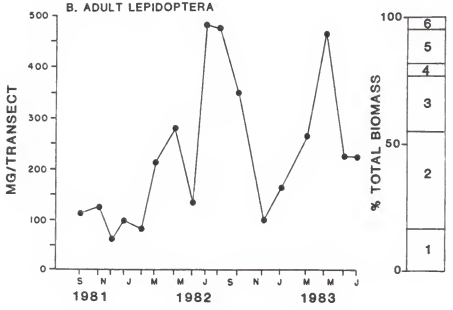
Seasonality and distribution of important groups

The seasonality and habitat distribution of arthropods varied across the 10 different groups (Figs. 3-5 a through j). Most of the arachnid biomass occurred in pastures, where spiders were an important component of the ground foliage fauna, especially in the late dry season (March-April) when pasture foliage was low, and in low elevation woods and edges, where harvestmen were abundant during wet months (Fig. 3-5a). Arachnids were a much less significant component in the fauna at higher elevations (cloud forests and gaps).

Adult Lepidoptera were most abundant during the early part of the rainy season in 1982 and 1983, but declined more rapidly in 1983, a dry El Niño year (Fig. 3-5b). They were particularly numerous in the most

Figure 3-5. Seasonal changes in total biomass of 10 arthropod groups, and the proportional occurrence of each arthropod group in six Monteverde habitats. Marks along bottom axis correspond to the midpoint of each sample period. Numbers in histograms refer to the following habitats: 1) pasture, 2) early successional shrub, 3) lower elevation woodland edge, 4) cloud forest gaps, 5) lower elevation woods, and 6) cloud forest. Letters on the horizontal axis refer to months of the year.


A. ARACHNIDA
MG/TRANSECT
140
100
60
20
S N J M M J S N J M M J
1981
1982
1983
% TOTAL BIOMASS
100
50
0
6
5
4
3
2
1


B. ADULT LEPIDOPTERA
MG/TRANSECT
500
400
300
200
100
0
S N J M M J S N J M M J
1981
1982
1983
% TOTAL BIOMASS
100
50
0
6
5
4
3
2
1

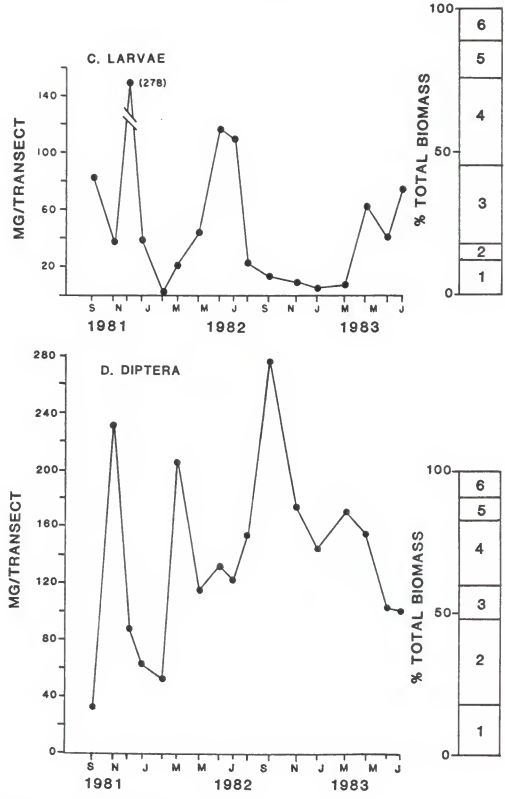


Figure 3-5 -- continued

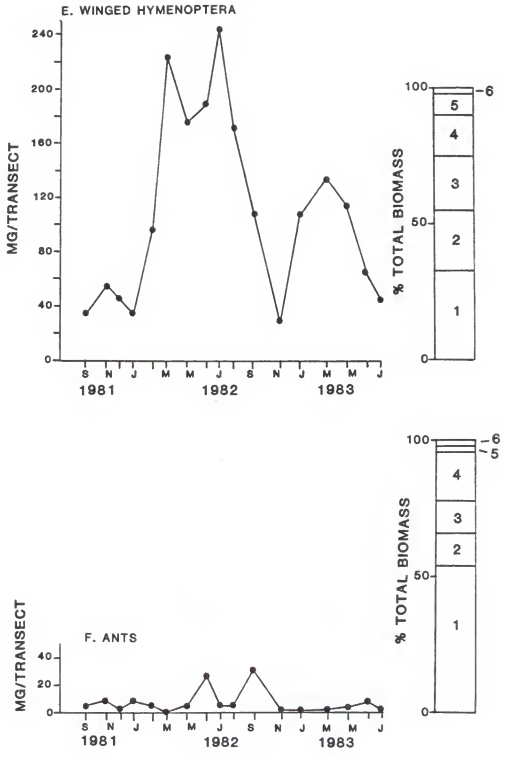


Figure 3-5 -- continued

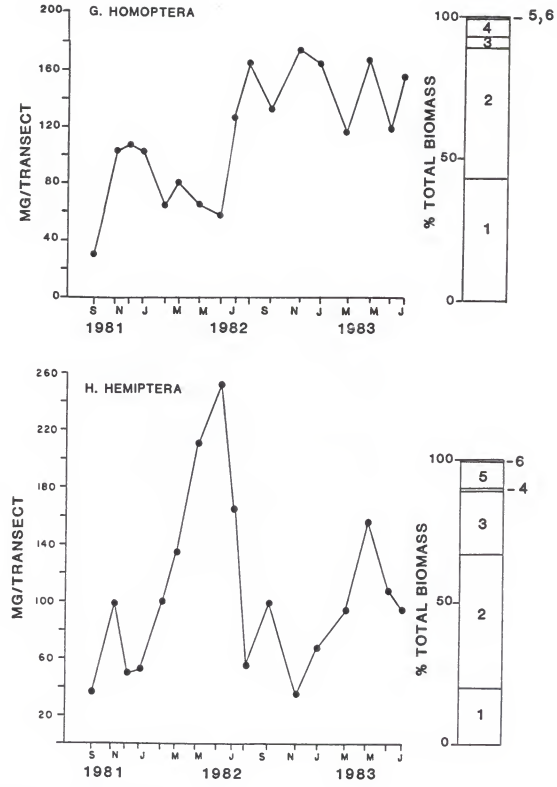


Figure 3-5 -- continued

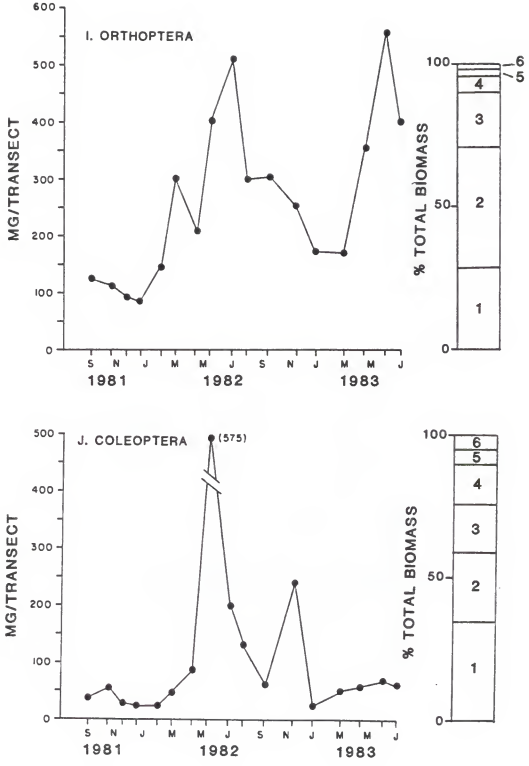


Figure 3-5 -- continued

heterogeneous habitats at lower elevations--successional areas, edges and second-growth woods. Biomass of larvae also peaked during the wet season, but their seasonality was more pronounced than that of the adults. Larvae were scarce in all habitats during the dry months (Fig. 3-5c). I found most larvae in heterogeneous edges and gaps at both high and low elevations. They were more common within forests than in open areas.

Diptera were always abundant in open habitats at all elevations, especially in the early secondary growth of shrubby areas and cloud forest gaps (Fig. 3-5d). The high biomass of flies in gaps resulted from larger individuals rather than greater abundance, as did peaks in the wet-dry transition periods, when the proportion of larger individuals increased. Because of their relatively small size and mobility, my sampling of Diptera was probably more sensitive to the effects of microclimate and microhabitat than for any other arthropods; this was reflected in the relatively eratic fluctuations I recorded in this group.

In contrast to the case with most other arthropods, I sampled the greatest biomass of flying Hymenoptera during the dry season (Feb-June); biomass stayed high in the early wet season of 1982 (Fig. 3-5e). Wasps and bees were most common in the open habitats, and decreased in abundance from open, drier habitats to higher and wetter areas. In general, ants (Fig. 3-5f) had the same habitat distribution as flying Hymneoptera; they were especially common in the logs and debris scattered throughout pastures. I sampled peaks in ant biomass during June and October of the 1982 wet season, but because I usually found

them in patchily distributed colonies, fluctuations in biomass were sensitive to chance encounters with large colonies.

I found significant numbers of Homoptera only in the most open habitats, especially at lower elevations where planthoppers and leafhoppers (Suborder Auchenorrhyncha: Superfamily Fulgoroidea; F. Cicadellidae) comprised a large proportion of the total biomass in pastures and early successional shrub (Fig. 3-5g). As with flies, the small size and mobility of hoppers made sampling much more sensitive to slight changes in microclimate and microhabitat; thus, I recorded relatively sporadic fluctuations in this group. Biomass of hoppers was lower during the dry season (Feb-June) than it was in each preceding wet season.

Hemiptera were uncommon in high elevation habitats, but during the dry season, they comprised a dominant component of the vegetationally diverse successional areas at lower elevations (Fig. 3-5h). Biomass of Hemipterans declined rapidly at the beginning of each rainy season. Secondary peaks that occurred in October-November of both years were due to the appearance of larger hemipterans in secondary woods and edges.

Orthopterans were most abundant in open habitats as well (Fig. 3-5i); they were one of the most important food sources for wrens in all habitats (see Chapter Four). Orthopteran biomass increased throughout the dry-wet season transition months, peaked during May and June, and then declined throughout the remainder of the wet season (Fig. 3-5i).

Coleopterans were more common in forest habitats than were most other arthropods. Biomass was highest during wet weather, and low during the early dry season (Fig. 3-5j). Fluctuations in beetle biomass were severe; more than any other group, the seasonality of Coleoptera

represented a composite of contrasting seasonal patterns of different families and species (see also Buskirk and Buskirk 1976). In addition, highly localized phenomena contributed to the fluctuations I measured. The large peak in June 1982, for example, resulted when I sampled large clumps of chrysomelid beetles in one pasture on one day. Except for this instance, Coleoptera were not usually dominant components of the pasture fauna.

Comparative diversity in arthropod groups

I calculated the dominance concentration, a Simpson diversity index (C (inv); Simpson 1949, Levins 1968, Whittaker 1975) for the 10 arthropod groups, by weight, on each transect within a habitat (Table A-2). C(inv) is directly proportional to diversity; the greater the value C(inv), the greater the diversity of arthropod groups.

$$C(inv) = \frac{1}{\sum_{i=1}^{s} \frac{n_i^2}{N}}$$

where N = the total importance values of all groups,
n(i) = the importance value of individuals in group i, and
s = the number of groups sampled.

I calculated C(inv) using the biomass of each group and omitted arthropods that were poorly represented in all habitats and/or in the diets of wrens (snails, millipedes, centipedes and all unidentified animals). I averaged the diversity indices for all transects (Table A-2) to obtain a mean C(inv) for the habitat during each sample period (Table 3-6).

Diversity of arthropod groups averaged significantly lower in the two forest habitats than in more open habitats (Kruskal-Wallis ANOVA, $H = 47.14$, $df = 5$, $P<0.001$); diversity was intermediate in gaps and on

Table 3-6. The average dominance concentration, C (inv), of arthropod groups on each transect within a habitat.

Habitat	Average C(inv) (n = 17 sample periods)	Standard Deviation	CV (%)
Pasture	3.49	0.471	13.5
Early successional shrub	3.48	0.357	10.2
Woodland edge	2.92	0.348	11.9
Cloud forest gaps	3.01	0.393	13.0
Low elevation woods	2.37	0.522	22.0
Cloud forest	2.73	0.415	15.2

edges. Furthermore, the relative degree of variation in the diversity indices over the 17 sample periods (CV) was significantly greater in low elevation woods than in other habitats (Miller Jacknife for CV, $F = 3.86$; $df = 5, 96$, $P<0.05$), and tended to be high in cloud forest as well. These results indicate that diversity of the 10 arthropod groups by weight was lower in forest habitats than in more open habitats, and that diversity changed relatively more over time in forests and woods, especially at lower elevations.

Changes in arthropod composition over time

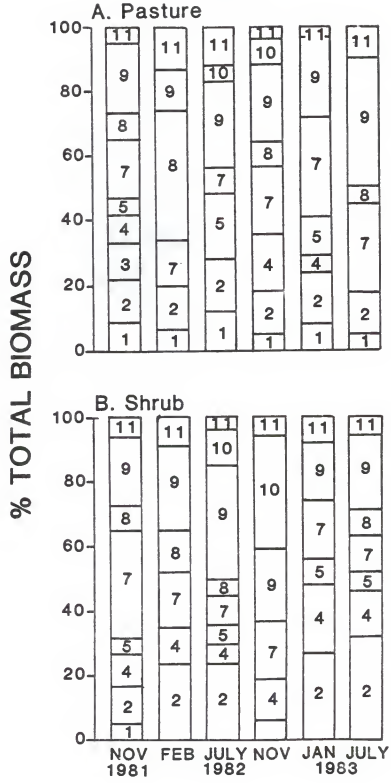
I investigated temporal variation in arthropod composition (by weight) using the proportional similarity index (Colwell and Futuyma 1971, Whittaker 1975, Feinsinger et al. 1981) to estimate turnover in the 10 arthropod groups in each habitat. Figs. 3-6 a through f show changes in arthropod composition for six of the 17 sample periods that occurred during dry-wet or wet-dry season transitions, when arthropod populations were most likely to change.

$$PS = 1 - 0.5 \sum_{1}^{i} p(i) - q(i)$$

where i = the total number of groups sampled,
p(i) = the proportion of group i in the first sample period, and
q(i) = the proportion of group i in the next sample period.

In this analysis, I computed the similarity index for the arthropod composition at a given site in consecutive sample periods; thus, I included only sites used throughout the 2 yrs of study. I averaged PS values over the sites within a habitat, and over all 17 sample periods to obtain a mean estimate of turnover in arthropod communities (Table 3-7). The proportional similarity averaged significantly lower in the two forest habitats than in other habitats (Kruskal-Wallis nonparametric

Figure 3-6. Turnover in the composition, by weight, of arthropod prey over six sample periods in six Monteverde habitats. Numbers in histograms refer to arthropod groups: 1) Arachnida, 2) adult Lepidoptera, 3) larvae, 4) Diptera, 5) flying Hymenoptera, 6) ants, 7) Homoptera, 8) Hemiptera, 9) Orthoptera, 10) Coleoptera, 11) all groups that each had less than 5% of the total biomass.


A. Pasture
B. Shrub
% TOTAL BIOMASS
100
80
60
40
20
0
NOV 1981
FEB
JULY 1982
NOV
JAN 1983
JULY

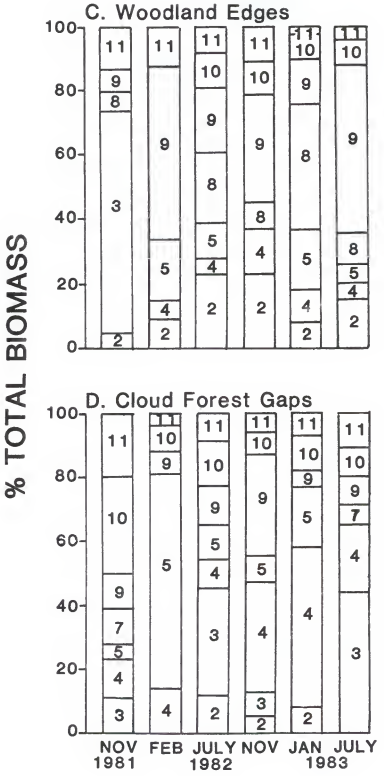


Figure 3-6 -- continued

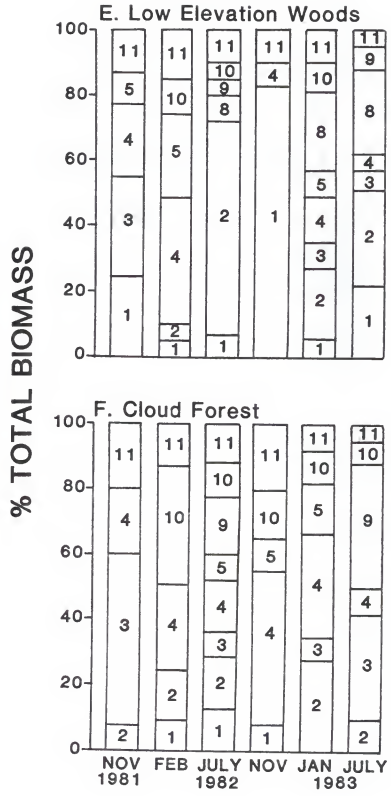


Figure 3-6 -- continued

Table 3-7. Proportional similarity in arthropod composition between consecutive sample periods.

Habitat	n (site-periods)	Mean PS between Consecutive Samples	Standard Deviation	CV (%)
Pasture	32	0.6083	0.1746	28.7
Successional shrub	32	0.6900	0.1180	17.1
Woodland edge	32	0.5614	0.1416	25.2
Cloud forest gaps	32	0.6164	0.1354	22.0
Low elevation woods	48	0.4743	0.2079	43.8
Cloud forest	48	0.5180	0.1612	31.1

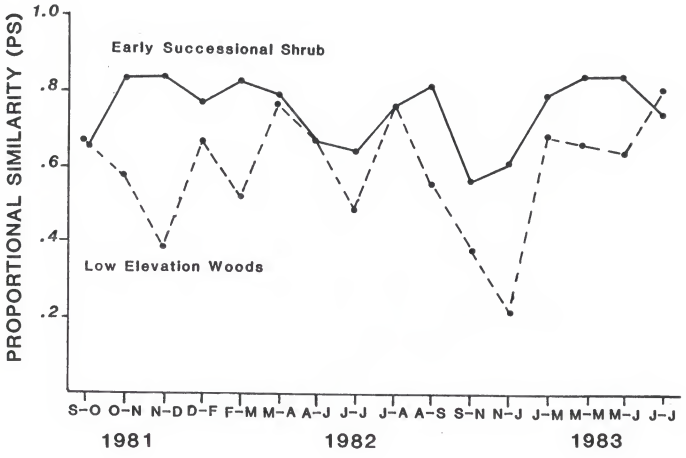
test, $H = 32.26$, $df = 5$, $P<0.01$). Figure 3-7 illustrates these differences for early successional shrub and low elevation woods. Whereas the composition of arthropod groups in open habitats remained relatively constant over time, turnover in forests was high. In general, open habitats supported a relatively high biomass of several orders of insects (Lepidoptera, Homoptera, Orthoptera), and these groups were likely to be a dominant part of the fauna all year (Figs. 3-6 a and b).

In contrast, forests, especially low elevation woods, were often dominated by one arthropod order in a given sample period, and this group changed over time (Figs. 3-6 e and f; e.g. July and November 1982 in low elevation woods, and November 1981 and February 1982 in cloud forest). In other sample periods, however, there was a more uniform distribution of biomass among several groups (e.g. January 1983 in low elevation woods and July 1982 in cloud forest).

Arthropod composition on woods edges and in gaps included elements from both adjacent open areas and forest; consequently, the turnover patterns there were more complex, but neither as high nor as variable as in the adjacent forests (Figs. 3-6 c and d).

Relative variation (CV) in proportional similarity was significantly greater in the two forests as well (Table 3-7; Miller Jacknife for variance: $F = 2.77$, $df = 5,186$, $P<0.05$; Miller Jacknife for CV: $F = 4.80$, $df = 5, 186$, $P<0.05$). Thus, not only was turnover in arthropod composition higher in forests, but the degree of turnover from one sample period to the next was much less predictable than in open habitats; turnover in forests was high in some periods (up to 80% change in composition) and very low (10%) in other periods. Relative variation

Figure 3-7. Proportional similarity in arthropod groups sampled in consecutive sample periods in early successional shrub and in low elevation woods. Letters on the horizontal axis refer to intervals between months.


PROPORTIONAL SIMILARITY (PS)
1.0
.8
.6
.4
.2
Early Successional Shrub
Low Elevation Woods
S–O O–N N–D D–F F–M M–A A–J J–J J–A A–S S–N N–J J–M M–M M–J J–J
1981
1982
1983

in arthropod turnover was also high in pasture, but this resulted from one sample period in which beetles constituted over 50% of the total biomass (see Fig. 3-6a).

Variation in arthropod composition over space

I investigated spatial variation in the composition of arthropods (using the 10 groups as above) by calculating the degree of similarity between the four adjacent transects at each site. I computed a proportional similarity index for each of the six possible pairwise combinations of the four transects at each site; I used the average PS of all combinations at all sites to estimate average inter-transect similarity for the entire habitat (Table A-3); thus, the number of PS values used in computing this mean was 24 for the year 1981-82 and 18 for 1982-83. The averages for all sample periods were pooled to obtain an overall mean PS (Table 3-8).

Similarity in arthropod composition among transects was significantly lower in low elevation woods and edges, and in cloud forest (Kruskal-Wallis nonparametric ANOVA; $H = 23.64$, $df = 5$, $P<0.05$). A bird foraging in one of these habitats would have encountered greater variability in the composition of prey as it moved within that habitat, than would a bird that was foraging in a more open habitat. Although the relative variance in proportional similarity was somewhat higher for the two forest habitats also, this difference was not statistically significant (Miller Jacknife F(variance) = 1.26, $df = 5,96$, $P>0.05$; F(CV) = 1.34, $df = 5,96$, $P>0.05$).

Table 3-8. Proportional similarity (PS) in arthropod compositon among transects within each habitat.

Habitat	Mean PS Among Transects (n = 17 sample periods)	Standard Deviation	CV (%)
Pasture	0.5679	0.1125	19.82
Successional shrub	0.5790	0.0795	13.72
Woodland edge	0.4462	0.0690	15.47
Cloud forest gaps	0.5506	0.0791	14.37
Low elevation woods	0.4627	0.1063	22.97
Cloud forest	0.5174	0.1087	21.00

Variability in Location of Prey Items

Diversity of substrates used by arthropods

Using the 10 substrate categories described in Methods, I calculated the diversity of substrates used by arthropods in each habitat using C(inv) for each sample period, as above. I averaged C(inv) estimates over all sample periods. For this analysis, I excluded substrates used by prey smaller than 5 mm because over 90% of these prey were superabundant and highly mobile Diptera, Homoptera or Coleoptera that were distributed fairly uniformly over all substrates at a given site. I restricted this analysis to larger prey that could be associated with specific substrates.

The diversity of substrates used by prey was significantly higher in low elevation woods and edges (Kruskal-Wallis nonparametric ANOVA; $H = 44.54$, $df = 5$, $P<0.05$), intermediate in the cloud forest habitats, and least in the most open habitats, especially pastures (Table 3-9). Thus, although low elevation woods and cloud forest contained less diverse prey types, these were spread over a greater diversity of substrates. Variance in substrate diversity over the 17 sample periods was significantly higher in low elevation woods as well (Miller Jacknife $F = 2.48$, $df = 5,96$, $P<0.05$), but relative variation (CV) did not differ significantly among habitats (Miller Jacknife $F = 1.45$, $df = 5,96$, $P>0.05$).

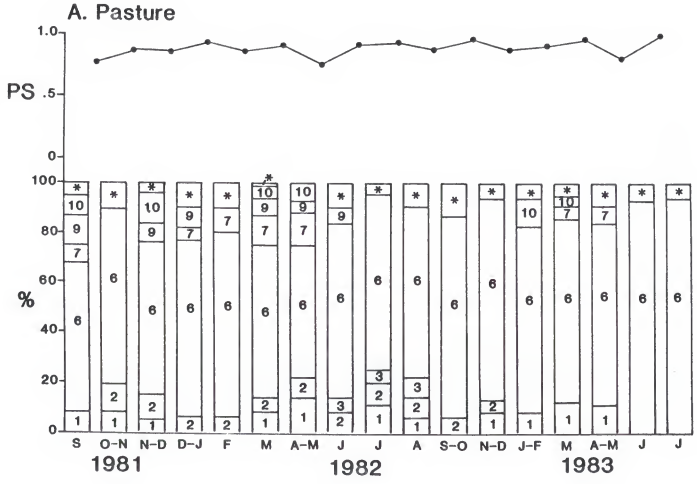
Temporal changes in substrate use

I investigated the relative degree of turnover in substrate use for different habitats using the proportional similarity index computed for proportional use of substrates over consecutive sample periods (Figs. 3-8 a through f).

Table 3-9. The diversity of substrates used by arthropods, estimated by C(inv), the dominance concentration.

Habitat	Mean C(inv) (n = 17 sample periods)	Standard Deviation	CV (%)
Pasture	1.94	0.5241	27.01
Successional shrub	2.95	0.8925	30.29
Woodland edge	4.09	0.8391	20.51
Cloud forest gaps	3.12	0.5927	18.98
Low elevation woods	3.78	1.1387	30.12
Cloud forest	3.42	0.6405	18.75

Figure 3-8. Temporal changes in the substrates used by arthropods (greater than 5 mm in length) in six Monteverde habitats, 1981 - 1983. Numbers in histograms refer to arthropod substrates: 1) air, 2) exposed foliage, 3) leaf undersides and stems, 4) leaf bracts and rolled leaves, 5) aerial leaf litter, 6) grass and herbaceous foliage, 7) ground litter, 8) twigs and branches, 9) logs, limbs and tree trunks, 10) woody crevices. Asterisks indicate all substrate categories, each having less than 5% of the total. Line graphs above histograms show temporal changes in the proportional similarity of arthropod substrates over consecutive sample periods. Letters on the horizontal axis refer to months of the year.


A. Pasture
PS
%
1.0
.5
0
100
80
60
40
20
0
S
O-N
N-D
D-J
F
M
A-M
J
J
A
S-O
N-D
J-F
M
A-M
J
J
1981
1982
1983

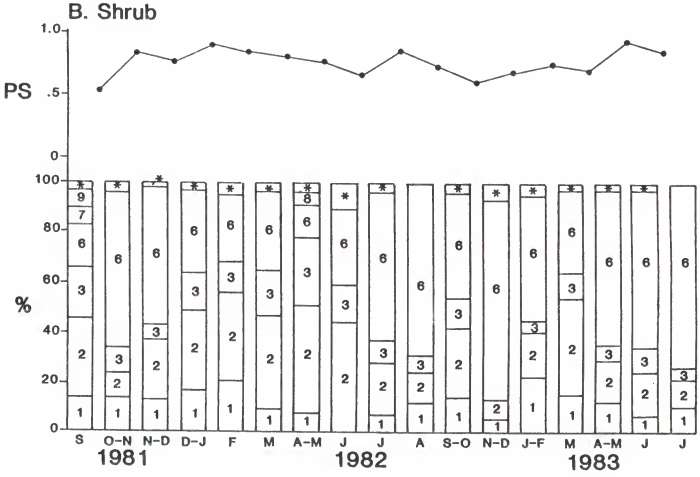


Figure 3-8 -- continued

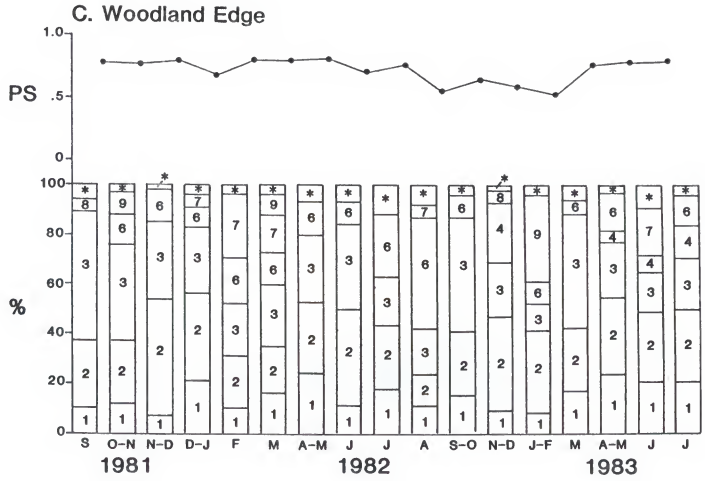


Figure 3-8 -- continued

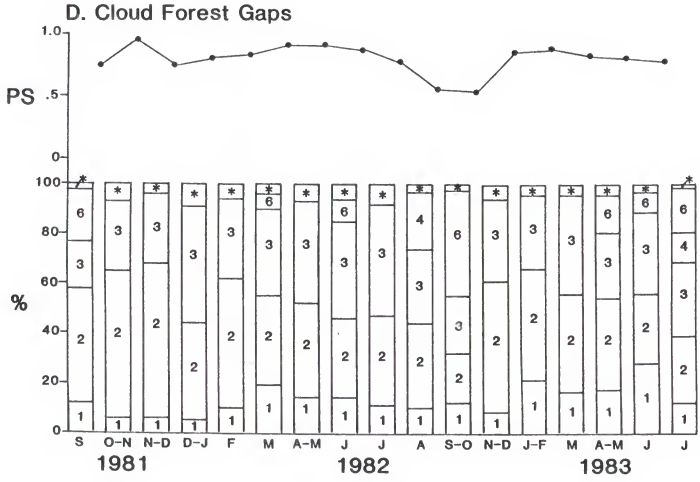


Figure 3-8 -- continued

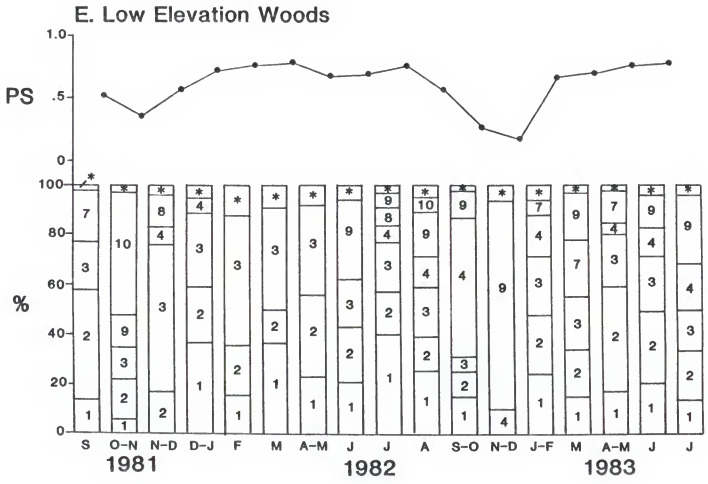


Figure 3-8 -- continued

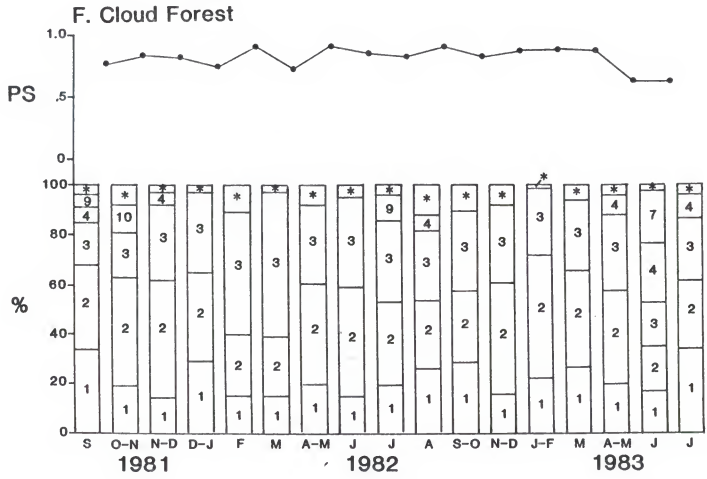


Figure 3-8 -- continued

The proportional similarity in substrate use averaged significantly lower in low elevation woods and edges, indicating a higher turnover in substrate use between contingent sample periods than in other habitats (Table 3-10; Kruskal-Wallis nonparametric ANOVA $H = 38.29$, $df = 5$, $P<0.001$). Not surprisingly, the homogeneous pastures showed little turnover in substrates used by prey (Fig. 3-8a). Most arthropods were predictably found in the ground foliage. Similarly, there was relatively little turnover in substrates used in early successional shrub and in both cloud forest habitats (Figs. 3-8b, 3-8d and 3-8f) and fluctuations in the degree of turnover were slight (CV, Table 3-10). On the other hand, the variance and CV in proportional similarity were significantly higher in low elevation woods, and to a lesser extent, on edges (Miller Jacknife; $F(\text{variance}) = 2.96$, $df = 5,90$; $P < 0.05$; $F(CV) = 4.08$, $df = 5,90$, $P < 0.05$) indicating that, whereas turnover in substrate use was high, the degree of turnover was variable, as compared with other habitats (Figs. 3-8c, 3-8e).

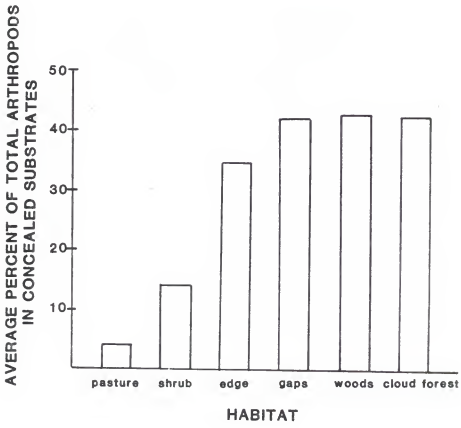
Prey in concealed microhabitats

Finally, I investigated prey concealment as a parameter that may affect food availability of wrens. At Monteverde, the average percent of total prey that I found in concealed microhabitats (see Methods: substrate categories include leaf undersides, concealed foliage, aerial leaf litter and woody crevices) increased significantly from the most open habitats to intermediate edges (Fig. 3-9; Kruskal-Wallis ANOVA; $H = 69.72$; $df = 5$, $P<0.05$), and averaged over 40% in both forest habitats (Table A-4). Since I restricted the analysis of substrate use to larger prey (> 5 mm in length), I did not include the tiny Homopterans that inhabited the low foliage of open habitats. Most hoppers were

Table 3-10. Proportional similarity (PS) in arthropod substrate use between consecutive sample periods.

Habitat	Mean PS (n = 17 sample periods)	Standard Deviation	CV (%)
Pasture	0.8802	0.0621	7.06
Successional shrub	0.7690	0.1059	13.77
Woodland edge	0.7201	0.0952	13.22
Cloud forest gaps	0.8018	0.1158	14.44
Low elevation woods	0.6083	0.1875	30.82
Cloud forest	0.8190	0.0886	10.82

Figure 3-9. The percent of arthropod prey in concealed substrates in six Monteverde habitats, averaged over 17 sample periods.


AVERAGE PERCENT OF TOTAL ARTHROPODS IN CONCEALED SUBSTRATES
50
40
30
20
10
pasture
shrub
edge
gaps
woods
cloud forest
HABITAT

cryptically colored, but so numerous and mobile that they were highly apparent. With the exception of pastures, low elevation woods had the highest relative variation (CV) in the proportion of hidden prey over time (Table A-4). At least 15%, and sometimes more than 70%, of the total prey in woods were in concealed microhabitats. Variation in this percent was very high for pastures (CV = 89%) also, but this reflected fluctuations within a range of 1-16% of the total prey in hidden microhabitats.

Discussion

Contrary to my original hypothesis, all of my estimates of temporal and spatial variance in arthropod populations were higher in forest habitats than in open habitats disturbed by man. I sampled far greater arthropod biomass and abundance, year-round, and less variation in this food supply over time and space, in open habitats compared to forests. The greater relative variation in the food supply in woods and forest depended on the lower prey biomass there because fluctuations in arthropod population parameters were more pronounced against the background of overall low availability. Higher rates of primary vegetative growth in open habitats may account for the higher arthropod biomass there (Janzen 1973, Schowalter 1985). Cutting and grazing maintained open habitats in a continual state of early succession and provided habitats for a multitude of colonizing arthropods. For the same reasons, edge habitats supported greater arthropod biomass than adjacent forest, but less than adjacent open habitats. Buskirk and Buskirk (1976) sampled arthropods with Malaise traps in forests and gaps near my study area at Monteverde, and found lower abundance in a forest interior as compared with a nearby gap edge. Janzen (1973) found higher

arthropod abundance and biomass in second growth habitats in lowland Costa Rica, as compared with adjacent forest, and Blake and Hoppes (1986) reported similar data from Illinois.

Seasonal changes in forests were more pronounced than in open habitats, and more pronounced in lower elevation woods than in higher elevation cloud forest. In Central America, a peak in insect populations at the beginning of the rainy season is tied to new vegetational growth; minimum arthropod levels generally occur in the middle of the dry season (Janzen and Schoener 1968, Robinson and Robinson 1970, Fogden 1972, Janzen 1973, Wolda 1978a,b, 1979, 1980, Smythe 1982, Tanaka and Tanaka 1982). This seasonality is more noticeable in areas with a strong dry season (Janzen and Schoener 1968, Robinson and Robinson 1970, Janzen 1973, Wolda 1978a, 1980, Levings and Windsor 1982). Although I expected open habitats at Monteverde to experience the most severe effects of the dry season, and although rainfall did fluctuate more in those areas, arthropod seasonality was indistinct, as compared with that in woods. In addition, periods of high biomass in woods and forest were more constricted in time, compared to adjacent edges. Some groups, especially Hymenoptera and Hemiptera, contributed to dry season peaks in open habitats; dry season peaks in arthropod abundance in open areas also were noted by Janzen (1973). Janzen (1973) sampled areas with a relatively mild dry season, as I did, and found that numbers and biomass of insects were more affected in forest than in adjacent second growth during the dry season. He attributed this to the drastic reduction in productivity of the foliage moving from secondary vegetation to adjacent forest understory.

At Monteverde, the more severe dry season at lower elevations apparently contributed to greater variance in arthropod parameters in woods compared to cloud forest above 1500 m. Janzen (1973) also noted higher variability in sweep samples from forests with more pronounced dry seasons than in wetter forests, and Wong (1986) reported that seasonal periods of low insect abundance were significantly longer in regenerating dipterocarp forests in Malaysia than in virgin forest at the same site. Although the effect of climate on vegetational growth and arthropod populations was probably the most important factor causing this variability, it is possible that the smaller tract size (i.e. the higher degree of fragmentation) of lower elevation woods contributed to arthropod population variability (Preston 1962, MacArthur and Wilson 1967, Willis 1979).

Different taxonomic groups may have different seasonal rhythms, (Janzen 1973, Buskirk and Buskirk 1976, Wolda 1978a, 1979, 1980, Levings and Windsor 1982, Smythe 1982, this study). Where overall arthropod biomass was low, especially in low elevation woods, variation in the seasonality of different arthropod taxa had the greatest impact on changes in overall abundance, biomass, and dispersion over space and substrates.

Whereas several orders of arthropods were always represented by relatively great biomass in open habitats, only a few groups (larvae and arachnids) comprised major parts of the biomass in forests, and these groups were highly seasonal and tended to occur in clumps. The occurrence of arthropod clumps was highly variable over time and space in woods; clumps were especially important during the wet season. In open habitats, however, both the proportion of total biomass in clumps

and the kinds of prey found in clumps were less important to wrens (see Chapter Four). I also measured greater turnover in the composition of arthropod biomass in forests, and greater variability in this composition from patch to patch within forests.

The relatively low diversity of arthropod groups in forests was spread over a greater diversity of substrate types, compared to open habitats. In addition, turnover in prey substrates was greater, and more variable over time, in forests. I found a greater proportion of arthropods on concealed substrates in woods and forest than I did in open habitats.

My results imply that wrens foraging in open habitats should encounter similar food availability from place to place, and from month to month, but that wrens foraging in forest habitats will encounter marked changes in the amount, types, and dispersion of arthropods, both seasonally, and from one patch to another. Furthermore, a greater proportion of prey will be in concealed microhabitats in forest, compared to open habitats. Wrens in low elevation woods should encounter greater variance in their food supply than wrens in wet cloud forest. Factors in addition to prey numbers and biomass--prey composition, dispersion, clumping, and substrates--should significantly affect food availability. Thus, contrary to my original predictions, wrens in forests, more than wrens in open, disturbed habitats, should have the greatest difficulty finding food, because forests, not open habitats, are the most variable places to search for food.

CHAPTER IV

VARIABILITY IN FORAGING BEHAVIOR

To investigate the initial hypothesis that wrens in open, disturbed habitats, HWs and PWs, should have greater flexibility in foraging behavior than forest wrens, RWs and GWs, I compared foraging behavior of the four wrens in the field and under experimental conditions. In the field, I measured both long-term seasonal changes in behavior and short-term variability in behavior over single foraging sequences of less than one hour. In addition, I compared short-term foraging variability of wrens during experiments in a controlled aviary habitat. I gathered data to answer the following questions: Which wrens show greater change in foraging behavior over time, and over different habitats? What components of foraging behavior account for these changes? Is behavioral variability dependent upon specific characterisitcs of the habitat? How are the changes related to variability in the food supply? I studied five aspects of foraging behavior: 1) foraging rates and the rate of change through foraging space, 2) breadth in the use of foraging space, 3) diversity in techniques used to capture prey, 4) diversity in substrates used to attack prey, and 5) diversity in the types and sizes of prey. I compared these five parameters among species using pooled data in all habitats, and data from one habitat, low elevation woodland edges, where I gathered observations on all four species. The aviary experiments provided additional information for comparisons among

species in the same habitat. I also compared foraging parameters within species across different habitats and seasons.

Methods

I recorded foraging behavior of individual wrens opportunistically, as I encountered them on searches through known territories; thus, all data are from focal animal sampling (Altmann 1974). I included data only from individuals that were actively foraging, and not singing, chasing neighbors, etc. My records included data from 46 HWs, 31 PWs, 22 RWs, and 35 GWs. About 80% of the total observations were from color-banded wrens. When I encountered a foraging wren, I recorded on tape every perch change and foraging movement while following the wren for as long as I could keep it in sight; thus, my recordings consisted of continuous timed sequences of the bird's movement, search tactics, and prey encounters. Sequences varied in length from 15 seconds to 40 minutes.

I recorded general data including date, time, weather, habitat type (as in Chapter III, Methods), bird identification, size and composition of foraging group, if present, and whether I initially located the wren by sight or by sound. I recorded changes in three foraging parameters -- microhabitat, height and perch type -- each with five categories. Foraging microhabitat categories were: 1) ground foliage or litter, 2) dead wood or woody vine tangles, 3) shrubs or green, leafy vine tangles, 4) edge or forest understory, and 5) trees. Height categories were: 1) less than 0.3 m, 2) 0.3 to 0.9 m, 3) 1.0 to 1.9 m, 4) 2.0 to 4.9 m, and 5) 5 or more m high. Perch type categories were: 1) twigs and branches less than 5 cm in diameter, 2) limbs and tree trunks more than 5 cm in diameter, 3) plant stems, 4) dead wood more than 5 cm in diameter, and

5) ground, ground litter, or short grass stems. I recorded every perch type as the wren landed on the perch.

I defined an attack as any maneuver directed at prey, whether successful or not. I defined the following six attack technique categories: 1) simple gleaning--wrens plucked stationary prey from substrates as they perched within 0 - 10 cm, 2) pouncing--wrens plucked stationary prey from substrates (usually leaf undersides and stems) as they jumped from their perch to strike, 3) hanging--wrens investigating aerial leaf litter, rolled leaves, or the leafy ends of branches hung while clinging sideways or upside-down in order to probe and tear open leaves concealing prey, 4) hawking--wrens flew up and/or out to strike at flying prey by making short, abrupt flights (less than 1 m) to the prey, then dropping back immediately to a perch, 5) hovering --wrens plucked stationary prey from a substrate while fluttering in the air within 1 - 5 cm of the prey, and 6) leaf-tossing--wrens flipped leaves and debris in ground litter, on the tops of logs, or suspended in aerial masses, to obtain concealed prey. I included all probes into concealed microhabitat surfaces (see categories for concealed substrates, Chapter III, Methods), but not exposed surfaces, as attacks.

I recorded the size length class (using the average bill length for each species as a reference) and type of prey captured using the categories listed in Chapter III, Methods. I could not identify 60% of all prey items taken by wrens in the field. I could identify some groups (e.g. larvae, Lepidoptera and Orthoptera) much more easily than others. However, since all wrens used a similar, broad array of arthropod groups (see Results), and because I detected no significant differences in prey sizes taken by different wrens in the field, I have

assumed that my biases in prey identification were similar across the four wren species.

I transcribed foraging sequences from tapes using a stopwatch, and subdivided the sequences into periods including 10 sequential perch changes each, to create equivalent sample units. I did not use sequences with fewer than 10 perch changes in analyses of foraging rates, but I recorded data for the first perch in each sequence. I used these single points as Foraging Point Observations and used them in analyses of foraging position diversity (see below).

I found no significant differences between years in foraging parameters, so I combined data for the two years. Thus, seasonal comparisons of foraging behavior include data from both wet seasons vs. both dry seasons.

Foraging Rates

I calculated the following four foraging rates from each 10-perch sample unit:

1) Foraging speed--the number of perches moved/second.

2) Attack rate--the number of attacks/second. When a wren used several strikes at the same substrate to extract a single prey item, e.g. from curled leaves, I counted the strikes as one attack.

3) Capture rate--the number of prey captures/second.

4) Changes in foraging position (CFP)--the sum of the number of category changes in each of three foraging parameters--microhabitat, perch height, and perch type (see categories above)--in a 10-perch sequence. A wren changing all three parameters at every perch would receive the maximum score of 30.

I used nonparametric statistical analyses to compare foraging rates

because my data were not normally distributed and standard transformations did not remove non-normality. In addition, variance in rates was dependent on the length of the foraging sequence. I analyzed differences among groups (e.g. species, seasons, habitats) in two ways. In the first method, I calculated the rate for each 10-perch sample unit, and because I often collected several dependent units from the same individual at the same place and time, I used only rates from the second 10-perch sequence in each case. I tested for differences in mean rates using Mann Whitney U tests (Siegel 1956). In the second method, I calculated a pooled mean for each category and tested for differences in the pooled means with the Cox and Lewis (1966) modification of the X^2 goodness of fit test:

$$X^2 = \frac{T}{N} \sum_{i=1}^{k} \frac{n^2_i}{t_i} - N$$

where n(i) = the total number of events performed by individuals in category i,
t(i) = the total time individuals were observed in category i,
K = the number of categories,
N = the sum of n(i), and
T = the sum of t(i).

In each comparison, the statistical significance was the same using both methods. Since the use of pooled means in Cox-Lewis tests incorporated all observations, but de-emphasized the higher variances associated with smaller sequences, I have included results of only the Cox-Lewis X^2 tests in the following Results section.

In addition, I estimated the relative breadth in each of the following four foraging parameters using the Simpson diversity index, C(inv) (see Chapter III, Methods) and tested for significant differences in the frequency distributions using G tests (Sokal and Rohlf 1981).

1) Breadth in foraging positions. I determined a matrix of 125 foraging modes representing all possible combinations of the five categories (see above) in each of three foraging parameters--microhabitat, perch height, and perch type. I assigned a unique mode number, representing each foraging position, to every fifth perch change of foraging sequences, and to each Foraging Point Observation. I pooled all mode numbers for each species and computed C(inv) based on these. Thus, a species with a high C(inv) was composed of individuals that I found over a large array of foraging positions, and a species with a low value was composed of individuals that I found in a limited number of foraging positions, relative to the number of positions available in their habitat. Only 72 of these modes were used by wrens in forests and edges, and only 59 were used by wrens in pastures and shrubs, so I normalized diversity estimates by dividing C(inv) by the maximum number of foraging positions (59 for HWs, and 72 for all other species).

2) Attack techniques. I pooled all attack techniques observed for each species and calculated C(inv) based on the proportional use of the six possible techniques listed above.

3) Prey substrates. I calculated C(inv) for relative breadth in substrate use by pooling category numbers within species for the proportional use of 10 substrate types where wrens attacked prey items (see Chapter III, Methods for substrate categories).

4) Prey types and sizes. I calculated C(inv) for diversity in prey types, using 10 prey categories (see Chapter III, Methods), and for diversity in prey size length classes using five size classes (see Chapter III, Methods). I analyzed data separately for prey captured during foraging sequences and for prey items brought to nests.

Aviary Experiments

I designed aviary experiments to test first, whether or not wrens in the same, controlled habitat would show the same behavioral differences I measured in the field and second, to further investigate relative flexibility in foraging behavior among different wrens. I constructed two aviaries, one holding cage and one experimental cage, each measuring 3.3 x 3.3 x 3.6 m high and situated side-by-side at the edge of a banana grove adjoining a strip of woodland edge at 1300 m elevation. Thus, my experimental site was located on a woodland edge, where all four species occurred naturally. I put a brushpile and some logs in the holding cage. In the experimental cage, I arranged a permanent foraging habitat consisting of a variety of substrates: logs, branches, aerial leaf litter, potted plants, and living saplings.

I captured wrens in mist nets during the non-breeding season, from 20 October 1982, to 28 February 1983. None of the wrens had brood patches or nests, and all were at least 6 months old. I put individuals in the holding aviary for a 24-hr adjustment period, allowing them to eat mealworms (Tenebrio beetle larvae) that I placed in a dish, and to forage for miscellaneous arthropods, which I captured with a sweep net every few hours. If a wren did not eat and/or if it continued to flit around the walls and corners of the cage rather than systematically search for insects, I released it at the capture site by the end of the first day. Individuals that I used for experiments included four RWs, and three each of HWs, PWs, and GWs.

Experiment I—foraging behavior in a controlled habitat. On the first morning after capturing a test wren, I used tan-colored thread to tie five mealworms (average live weight = 2 g) to each of the following

nine substrates in the experimental cage: 1) leaf tops and undersides more than 1 m high, 2) twigs and branches (any height) less than 2 cm in diameter, 3) leaves in the ground litter, 4) leaf tops and undersides less than 10 cm high, 5) inside leaf bracts less than 1 m high, 6) exposed woody surfaces (any height) more than 5 cm in diameter, 7) concealed wood crevices and holes (any height), 8) inside dead aerial leaf litter more than 1 m high, and 9) suspended in the air from thin monofilament fishing line (more than 1 m high). I mapped each prey location in three dimensions and used exactly the same spots for experiments of all wrens. I also classified each location as concealed or exposed; 18 (40%) of the prey locations were concealed.

I released the wren into the test aviary and recorded all foraging movements on tape in the manner described above for field observations. I calculated foraging speed as for field data, ignoring time the bird was not foraging or was out of view. In addition, I calculated three estimates of response: the total number of prey captured, the capture rate (number of prey/time spent foraging in view), and the average time between prey captures. I recorded movements between, and time spent in, each of five microhabitats--ground litter, log surfaces, leafy foliage more than 1 m high, leafy foliage at ground level, and woody vine tangle (which included the prey locations in aerial leaf litter). I caught the bird after 3 hrs of recorded foraging time and removed all leftover mealworms in prepartion for Experiment II.

Experiment II--changes in the distribution of prey items over four trial periods. I designed the second experiment to compare the responses of wrens to a change in the substrates of prey items. I ran four trials in the same sequence for each wren. Two hours after

completion of Experiment I, I hid 12 mealworms in mapped locations in aerial leaf litter and recorded the wren's foraging behavior for 2 hrs, as above. I removed leftover mealworms, left the bird alone for 1 hour, then hid 12 mealworms in log surfaces and repeated the observations. I ran the third and fourth trials, with mealworms hidden in leaf bracts and ground litter, respectively, on the following morning. For each trial, I calculated three estimates of response: the capture rate, the average time required to find the first prey item, and the average time between prey captures.

Experiment III--response to a novel foraging situation. In the final experiment, carried out 1 hr after completing Experiment II, I compared the response of wrens to a novel foraging substrate, 4 cm-diameter tomato sauce cans. I taped one mealworm each to the inside of each of 10 cans that had both ends removed, and placed the cans in mapped locations. I recorded the foraging behavior of the wren for the next 2 hrs and calculated four estimates of response: the total number of prey found, the capture rate, the average foraging time required to discover the first prey item, and the average time between prey captures. After the third experiment I released the wrens where I had captured them.

Results

Foraging Rates--Movement Through the Habitat

Comparisons among species

The two smaller species, HWs and GWs, moved faster, had higher attack rates, and higher rates of change in foraging position than the two larger species, PWs and RWs (Table 4-1). Faster movement was correlated with a greater rate of change in foraging position (CFP).

Table 4-1. Foraging rates of neotropical wrens, with data from all habitats pooled.

	Wren Species				
	HW	PW	RW	GW	Cox-Lewis X^2
Number of 10-perch sequences (n)	442	413	117	249	---
Perches/sec	0.523	0.372	0.421	0.543	346.09[a]
Attacks/sec	0.062	0.037	0.024	0.062	149.67[a]
Captures/sec	0.014	0.011	0.007	0.012	15.37[a]
CFP[b]	1.84	1.03	1.64	1.84	110.10[a]

[a]All Cox-Lewis tests significant at $P < 0.05$ with 3 df.

[b]See Changes in Foraging Position; see Chapter Four, Methods for method of estimation.

PWs seldom changed foraging position compared to other wrens, and RWs had the lowest attack and capture rates of all wrens.

I compared foraging rates of wrens in one habitat, low elevation woodland edges, where I had observations for all four species (Table 4-2) and, in general, obtained the same results. The smaller HWs and GWs moved faster, and attacked prey more often, than PWs and RWs. Again, PWs changed foraging position much less often than the other species, and RW capture rates remained lower than those of the other wrens.

In addition, I compared foraging rates for pairs of species that foraged in the same habitat; the results were similar to those in which data from all habitats were pooled. In early successional shrub, the smaller HWs moved faster and attacked more often than PWs, but there was no significant difference in capture rates or CFPs of the two species (Table 4-3a). PWs and RWs moved at the same speed when in the same habitat, woodland edges, but PWs seldom altered their foraging position, and attacked and caught significantly more prey than RWs (Table 4-3b). Sample sizes for GWs foraging in lower elevation habitats were small, so I combined data for GWs from both woods and edges in order to compare them with RWs in the same two habitats. GWs moved faster and attacked more often than RWs in low elevation woods and edges, but CFPs and capture rates for the two species were not significantly different (Table 4-3c).

Within species comparisons--variability in foraging rates between habitats

HWs moved faster, changed foraging positions more often, and attacked more often when in open pastures compared to other habitats, but their capture rates were similar across habitats (Table 4-4a). PWs

Table 4-2. Foraging rates of four neotropical wrens on woodland edges.

	Wren Species				
	HW	PW	RW	GW	Cox-Lewis X^2
Number of 10-perch sequences (n)	32	211	56	12	---
Perches/sec	0.568	0.388	0.417	0.524	48.69[a]
Attacks/sec	0.049	0.041	0.026	0.059	13.89[a]
Captures/sec	0.014	0.013	0.006	0.003	8.27[a]
CFP[b]	1.69	0.70	1.66	1.33	59.02[a]

[a]All Cox-Lewis tests significant at $P < 0.05$ with 3 df.

[b]Changes in Foraging Position; see Chapter Four, Methods for method of estimation.

Table 4-3. Foraging rates of wren species pairs in the same habitats. a) House Wrens and Plain Wrens in early successional shrub; b) Plain Wrens and Rufous-and-white Wrens on woodland edges; c) Rufous-and-white Wrens and Gray-breasted Wood-Wrens in low elevation woods and edges.

	Wren Species		
a)	HW	PW	Cox-Lewis X^2
Number of 10-perch sequences (n)	63	202	---
Perches/sec	0.444	0.357	22.70[a]
Attacks/sec	0.053	0.032	16.15[a]
Captures rate	0.014	0.010	1.82 NS
CFP[b]	1.44	1.37	0.01 NS
b)	PW	RW	
Number of 10-perch sequences	211	56	---
Perches/sec	0.388	0.417	1.92 NS
Attacks/sec	0.041	0.026	8.82[a]
Captures/sec	0.013	0.006	5.18[a]
CFP[b]	0.700	1.66	45.33[a]
c)	RW	GW	
Number of 10-perch sequences (n)	117	36	---
Perches/sec	0.421	0.532	14.82[a]
Attacks/sec	0.024	0.053	17.61[a]
Captures/sec	0.007	0.004	0.68 NS
CFP[b]	1.64	1.33	1.60 NS

[a]Cox-Lewis tests significant at $P < 0.05$ with 1 df; NS = not significant.

[b]Changes in Foraging Position; see Chapter Four, Methods for method of estimation.

Table 4-4. Foraging rates of wrens in different habitats. a) House Wrens; b) Plain Wrens; c) Rufous-and-white Wrens; d) Gray-breasted Wood-Wrens in cloud forest and gaps; d) Gray-breasted Wood-Wrens in low vs. high elevation habitats; e) Gray-breasted Wood-Wrens in low and high elevation habitats.

a)	Pasture	Shrub/Edge	Cox-Lewis X^2
Number of 10-perch sequences (n)	347	95	---
Perches/sec	0.537	0.478	9.50[a]
Attacks/sec	0.065	0.052	5.11[a]
Captures/sec	0.015	0.014	0.21 NS
CFP[b]	1.92	1.53	6.31[a]
b)	Shrub	Woodland Edge	
Number of 10-perch sequences (n)	202	211	---
Perches/sec	0.357	0.388	6.44[a]
Attacks/sec	0.032	0.041	8.06[a]
Captures/sec	0.010	0.013	2.61 NS
CFP[b]	1.37	0.700	45.15[a]
c)	Woodland Edge	Low elev. Woods	
Number of 10-perch sequences (n)	56	61	---
Perches/sec	0.417	0.424	0.82 NS
Attacks/sec	0.026	0.022	0.65 NS
Captures/sec	0.006	0.007	0.02 NS
CFP[b]	1.66	1.62	0.15 NS

Table 4-4 -- continued

d)	Gaps	Cloud Forest	Cox-Lewis x^2
Number of 10-perch sequences (n)	81	168	---
Perches/sec	0.556	0.539	0.51 NS
Attacks/sec	0.072	0.058	3.58[a]
Captures/sec	0.015	0.010	2.16 NS
CFP[b]	1.63	1.94	2.81 NS
e)	Low Elevation Woods/Edges	High Elevation Gaps/Cloud Forest	
Number of 10-perch sequences (n)	36	249	---
Perches/sec	0.532	0.544	0.24 NS
Attacks/sec	0.053	0.062	0.85 NS
Captures/sec	0.004	0.012	3.39[a]
CFP[b]	1.33	1.84	4.54[a]

[a]Cox-Lewis tests significant at $P < 0.05$ with 1 df; NS = not significant.

[b]Changes in Foraging Position; see Chapter Four, Methods for method of estimation.

moved somewhat faster, but seldom changed foraging position, on woodland edges compared to early successional shrub. PWs typically concentrated their searching in aerial leaf litter when they foraged on woodland edges; they moved quickly between patches of leaf litter, but remained in similar foraging modes for long periods. Capture rates of PWs were similar in both habitats (Table 4-4b). I found no difference in foraging rates or CFPs among RWs between woods and edges (Table 4-4c). GWs moved slightly faster and attacked more often when in gaps compared to cloud forest, but their capture rates did not differ significantly between the two habitats (Table 4-4d). In contrast, GW capture rates and CFPs were significantly lower in low elevation habitats than in cloud forest and gaps, even though foraging rates of GWs in the two areas were similar (Table 4-4e).

Within species comparisons--variability in foraging rates between seasons

Foraging speed, attack rates, and CFPs of wrens were more likely to differ between wet and dry seasons than were capture rates. HWs, PWs and RWs foraged significantly slower during the dry season, and GWs moved slightly slower in the dry season as well (Table 4-5 a-d). For HWs, PWs, and GWs the slower speeds were accompanied by increased attack rates, but RWs attacked prey much less frequently in the dry season than in the wet season. All species changed foraging positions more often during the dry season, although these differences were insignificant for PWs and RWs. Thus, in general wrens tended to slow down, change foraging position more often, and attack more often when food availability was lower in most habitats, during the dry season. Capture rates for all species tended to be lower in the dry season, but all seasonal differences were insignificant (Table 4-5a-d).

Table 4-5. Foraging rates of neotropical wrens in wet vs. dry seasons. a) House Wrens; b) Plain Wrens; c) Rufous-and-white Wrens; d) Gray-breasted Wood-Wrens.

a) House Wrens	wet	dry	Cox-Lewis X^2
No. sequences (n)	271	171	---
Perches/sec	0.554	0.484	20.06[a]
Attacks/sec	0.057	0.069	5.14[a]
Captures/sec	0.016	0.012	1.61 NS
CFP[b]	1.71	2.04	6.29[a]
b) Plain Wrens			
No. sequences (n)	200	213	---
Perches/sec	0.413	0.340	38.54[a]
Attacks/sec	0.035	0.038	0.67 NS
Captures/sec	0.012	0.011	0.30 NS
CFP[b]	0.935	1.174	3.48 NS
c) Rufous-and-white Wrens			
No. sequences (n)	93	24	---
Perches/sec	0.454	0.329	20.18[a]
Attacks/sec	0.029	0.011	10.36[a]
Captures/sec	0.008	0.003	2.73 NS
CFP[b]	1.59	1.83	0.66 NS

Table 4-5 -- continued

d) Gray-breasted Wood-Wrens	wet	dry	Cox-Lewis X^2
No. sequences (n)	219	30	---
Perches/sec	0.547	0.527	0.67 NS
Attacks/sec	0.057	0.098	15.33[a]
Captures/sec	0.012	0.011	0.07 NS
CFP[b]	1.77	2.37	5.22[a]

[a]Cox-Lewis tests significant at $P < 0.05$ with 1 df.

[b]Changes in Foraging Position; see Chapter Four, Methods for method of estimation.

Diversity in Foraging Positions

Comparisons among species

I found greater diversity in the use of foraging space by GWs than by other wrens when I compared normalized C(inv) values for pooled data from all habitats (Fig. 4-1); GWs foraged over a broad array of heights, from ground level through forest understory, woody tangles and trees. PWs used the narrowest range of positions, foraging primarily under 5 m high in the dense, leafy foliage of trees and shrubs.

I controlled for the influence of different habitats by comparing the normalized C(inv) of different species in the same habitat (Table 4-6). On woodland edges, where GWs used fewer foraging positions than they did at higher elevations, HWs had the highest values of C(inv). Again, PWs used the least variety of foraging positions, consistent with their low CFPs on woodland edges. HWs also had a greater diversity index than PWs in early successional shrub. GWs in high elevation forests and gaps had greater diversity indices than RWs in woods and woodland edges, respectively, but GW indices in low elevation woods, based on only a few samples, were extremely low.

Within species comparisons--diversity of foraging positions in different habitats

Both open habitat wrens, HWs and PWs, used a greater diversity of foraging positions in heterogeneous shrub habitat compared to pastures and/or woodland edges (Table 4-6). The two forest species, RWs and GWs, used a greater diversity of foraging positions within forests than they did on edges. GWs in cloud forest used a greater variety of foraging positions than any other species in any habitat, but this breadth decreased markedly at lower elevations. This may have resulted from the

Figure 4-1. Use of foraging space by four neotropical wrens. Sample sizes and diversity estimates, based on normalized values of C(inv), are as follows: HW = House Wren (n = 1501, C(inv) = .1828), PW = Plain Wren (n = 1542, C(inv) = .1672), RW = Rufous-and-white Wren (n = 497, C(inv) = .1800), GW = Gray-breasted Wood-Wren (n = 888, C(inv) = .3132). Each small square represents a unique foraging mode, based on three foraging parameters: microhabitat, perch height, and perch type. Microhabitat categories are: 1) ground foliage or litter, 2) dead wood or woody vine tangles, 3) edge or forest understory, 4) shrubs or green, leafy vine tangles, and 5) trees. Perch height categories are: 1) less than 0.3 m, 2) 0.3 to 0.9 m, 3) 1.0 to 1.9 m, 4) 2.0 to 4.9 m, 5) 5 or more m high. Perch type categories are: 1) t/b = twigs and branches less than 5 cm in diameter, 2) li/tr = limbs and tree trunks more than 5 cm in diameter, 3) st = plant stems, 4) wd = dead wood more than 5 cm in diameter, and 5) g = ground, ground litter, or short grass stems.

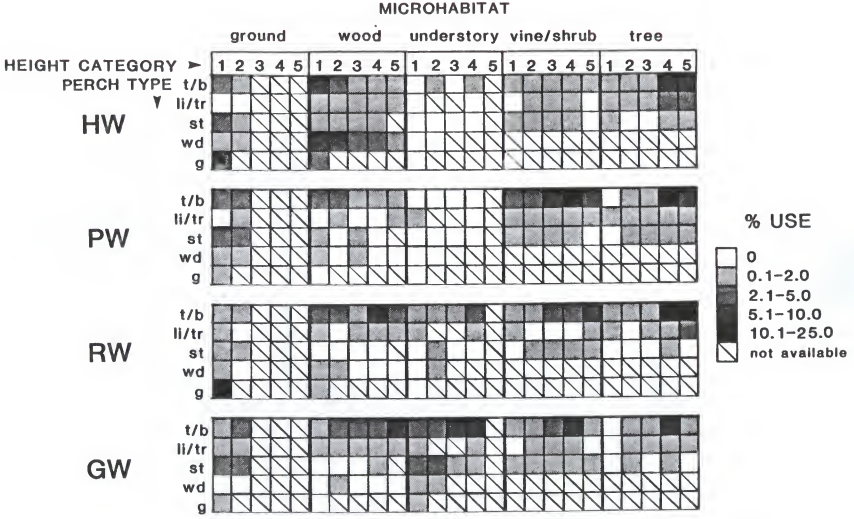

MICROHABITAT
ground
wood
understory
vine/shrub
tree
HEIGHT CATEGORY ►
1 2 3 4 5
PERCH TYPE
t/b
li/tr
st
wd
g
HW
PW
RW
GW
% USE
0
0.1–2.0
2.1–5.0
5.1–10.0
10.1–25.0
not available

Table 4-6. The diversity of foraging positions used by wrens in different habitats.

Wren Spp.		Habitat				
		Pasture	Shrub	Woodland Edge	Gap	Woods	Cloud Forest
HW	C(inv)	0.1668	0.2230	0.1935			
	(n)	(1032)	(348)	(121)			
PW	C(inv)		0.2187	0.1116			
	(n)		(809)	(733)			
RW	C(inv)			0.1460		0.1829	
	(n)			(255)		(242)	
GW	C(inv)			0.0970	0.1690	0.1068	0.2722
	(n)			(35)	(284)	(65)	(504)

(n) = the total number of foraging positions used to calculate the normalized value of C(inv).

smaller samples for GWs there, but it is consistent with the drop in CFP at low elevation sites discussed above.

Within species comparisons--diversity of foraging positions in different seasons

I compared diversity estimates between wet and dry seasons to determine if wrens changed their use of foraging space between seasons (Table 4-7). The three wrens in the lower and drier habitats, HWs, PWs, and RWs, used a greater diversity of positions during the dry season. But the greatest seasonal change in spatial diversity was achieved by GWs, which used a greater diversity of foraging positions in the wet season.

Techniques used to Attack Prey

Comparisons among species

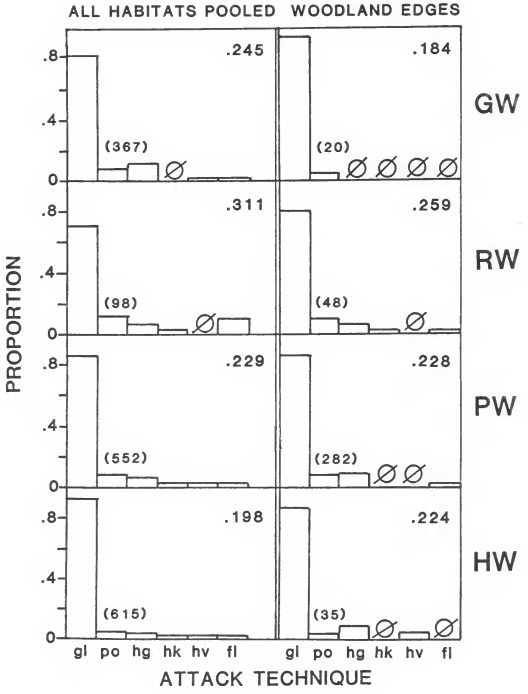
The proportional use of six attack techniques differed significantly among the four wrens (G for pooled habitats = 83.18, df = 15, $P < 0.005$). All species used simple gleaning more than 70% of the time, but the two forest wrens, especially RWs, used other techniques more frequently than the open habitat wrens, and consequently, had higher diversity indices (Fig. 4-2). These differences were reduced when I compared techniques used by species in the same habitat, woodland edges (Fig. 4-2), but remained significantly different if I eliminated the rare technique categories -- hawking, hovering, and flipping leaves (G for woodland edges = 14.46, df = 6, $P < 0.05$). On woodland edges, RWs used a greater diversity of attack techniques than did the other three species.

Table 4-7. Seasonal differences in the diversity of foraging positions used by four neotropical wrens.

	Season			
	wet		dry	
Wren Spp.	C(inv)	n	C(inv)	n
HW	0.185	880	0.204	621
PW	0.155	833	0.169	709
RW	0.157	371	0.162	126
GW	0.317	782	0.196	106

C(inv) = the normalized dominance concentration; n = the total number of foraging positions used to calculate C(inv).

Figure 4-2. Techniques used by four neotropical wrens to attack prey. HW = House Wren, PW = Plain Wren, RW = Rufous-and-white Wren, GW = Gray-breasted Wood-Wren. Technique abbreviations are: gl = glean, po = pounce, hg = hang, hk = hawk, hv = hover, fl = flip leaves. The numbers in parentheses in the lower left corner of each graph are the sample sizes (total number of attack techniques observed). The numbers in the upper right corner of each graph are the normalized values of C(inv) and estimate relative diversity in use of techniques. Circles with slashes represent zeroes.


ALL HABITATS POOLED
WOODLAND EDGES
PROPORTION
.8
.4
0
.245
(367)
.184
(20)
GW
.311
(98)
.259
(48)
RW
.229
(552)
.228
(282)
PW
.198
(615)
.224
(35)
HW
gl po hg hk hv fl
gl po hg hk hv fl
ATTACK TECHNIQUE

Within species comparisons--attack techniques used in different habitats

Of the four wrens, only GWs showed a significant difference in their use of attack techniques in different habitats (G for HWs = 8.12, G for PWs = 8.67, G for RWs = 7.83, G for GWs = 18.00, df = 5, $P < 0.01$ for GWs). GWs used a greater diversity of techniques, in addition to their broader use of foraging space, in cloud forest compared to gaps (Fig. 4-3). In particular, GWs used pouncing and hanging to attack prey on leaf undersides, stems, and in curled leaves, more than any species in any habitat. RWs also used a wider variety of techniques, especially leaf-flipping, within woods compared to edges, but the differences were statistically insignificant.

Within species comparisons--attack techniques used in different seasons

Two species, GWs and HWs, used a significantly different distribution of techniques in wet and dry seasons (Fig. 4-4; G for HWs = 17.22, G for PWs = 5.93, G for RWs = 2.67, and G for GWs = 12.40, df = 5, $P < 0.05$ for HWs and GWs). HWs and GWs used pouncing and hanging techniques more during the wet season. For GWs, this was correlated with the use of a greater variety of foraging positions in the wet season compared to the dry season.

Diversity of Prey Substrates Attacked by Wrens

Species comparisons

The frequency distributions for prey substrates attacked by wrens were significantly different among the four wren species (Fig. 4-5; G for pooled habitats = 768.41, df = 24, $P < 0.01$). RWs used the broadest variety of substrates, commonly attacking prey on leaf surfaces, woody substrates, and aerial leaf litter. HWs, which used the greatest

Figure 4-3. Techniques used by four neotropical wrens to attack prey in different habitats. Abbreviations and symbols are the same as for Figure 4-2. The numbers in parentheses in the lower left corner of each graph are the sample sizes. The numbers in the upper right corner of each graph are the normalized values of C(inv) and estimate relative diversity in use of techniques.

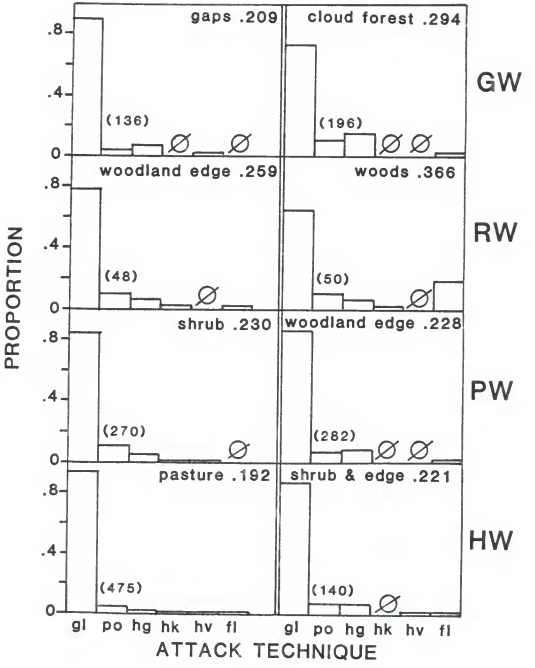

gaps .209
cloud forest .294
GW
(136)
(196)
woodland edge .259
woods .366
RW
(48)
(50)
shrub .230
woodland edge .228
PW
(270)
(282)
pasture .192
shrub & edge .221
HW
(475)
(140)
.8
.4
0
PROPORTION
gl po hg hk hv fl
gl po hg hk hv fl
ATTACK TECHNIQUE

Figure 4-4. Techniques used by four neotropical wrens to attack prey in the wet and dry seasons. Abbreviations and symbols are the same as for Figure 4-2. The numbers in parentheses in the lower left corner of each graph are the sample sizes. The numbers in the upper right corner of each graph are the normalized values of C(inv) and estimate relative diversity in use of techniques.

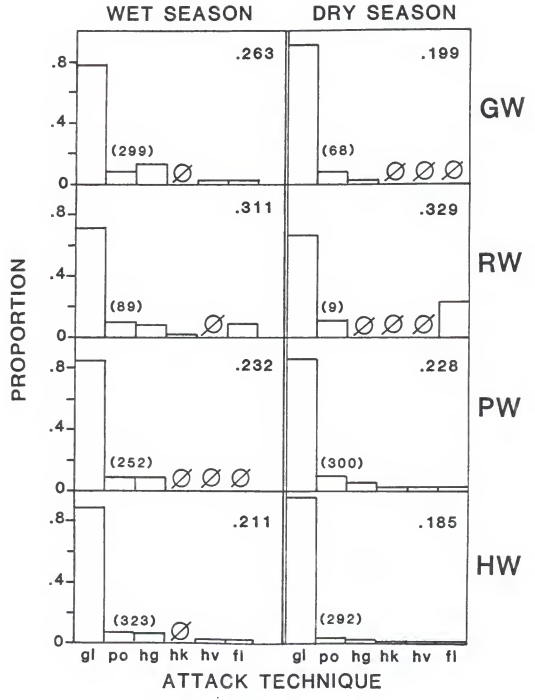
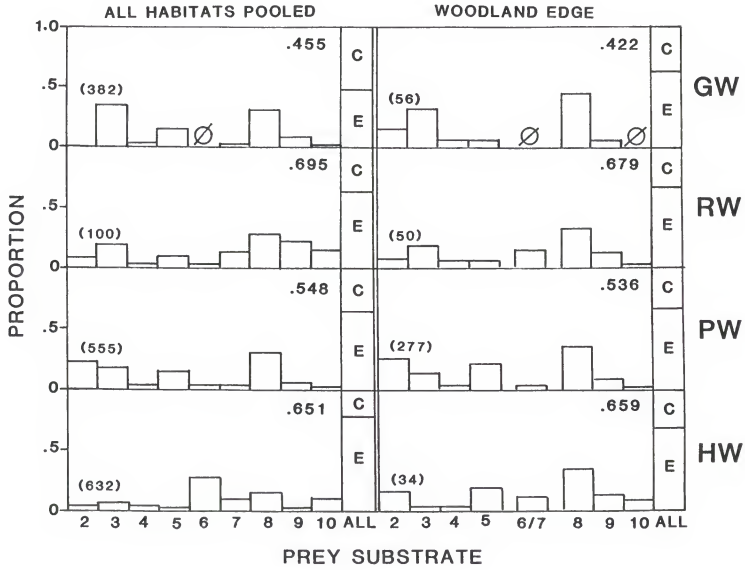

WET SEASON
DRY SEASON
PROPORTION
.8
.4
0
.263
(299)
.199
(68)
GW
.311
(89)
.329
(9)
RW
.232
(252)
.228
(300)
PW
.211
(323)
.185
(292)
HW
gl po hg hk hv fl
gl po hg hk hv fl
ATTACK TECHNIQUE

Figure 4-5. Prey substrates attacked by four neotropical wrens. Substrate categories are: 2) exposed foliage, 3) leaf undersides and stems, 4) leaf bracts and rolled leaves, 5) aerial leaf litter, 6) grass and herbaceous foliage, 7) ground litter, 8) twigs and branches, 9) logs, limbs, and tree trunks, 10) woody crevices, and ALL = all substrates combined. (Wrens did not use substrate category 1) air). Bars on the far right of each graph labelled E = exposed substrates (categories 2, 6, 7, 8, and 9) and C = concealed substrates (categories 3, 4, 5, and 10) show the proportion of attacks directed at exposed vs. concealed substrates. The numbers in parentheses in the lower left of each graph are the sample sizes (total number of attacks). The numbers in the upper right corner of each graph are the normalized values of C(inv) and estimate relative diversity in use of prey substrates. Circles with slashes represent zeroes.


ALL HABITATS POOLED
WOODLAND EDGE
PROPORTION
1.0
.5
0
.455
.422
.695
.679
.548
.536
.651
.659
(382)
(56)
(100)
(50)
(555)
(277)
(632)
(34)
C
E
GW
RW
PW
HW
2 3 4 5 6 7 8 9 10 ALL
2 3 4 5 6/7 8 9 10 ALL
PREY SUBSTRATE

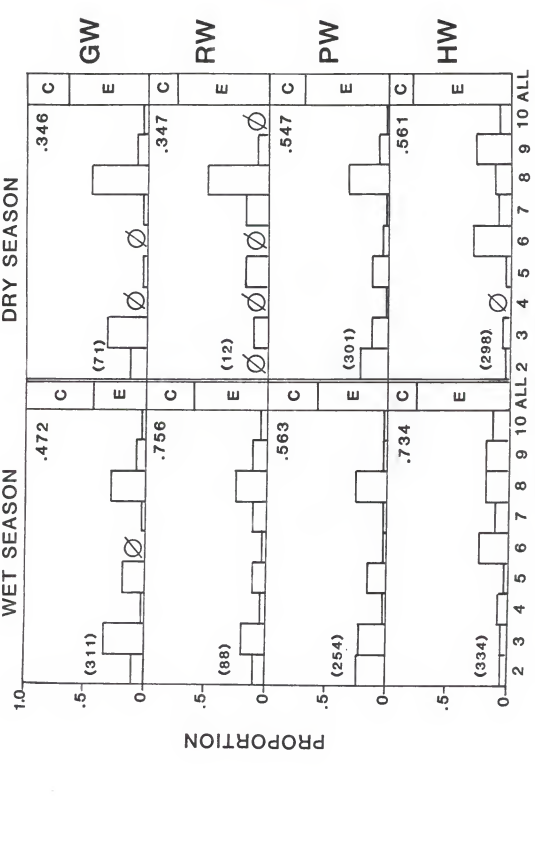
proportion of exposed substrates, attacked prey primarily in low grass, on log surfaces and in crevices, and on twigs and branches in logpiles, in accordance with the most common substrates in the pastures where HWs spent most of their time. In contrast, PWs concentrated on leaf surfaces, twigs, and aerial leaf litter. GWs attacked prey on concealed substrates more than 50% of the time, significantly more often than the other species (Fig. 4-5; G for pooled habitats = 90.58, df = 3, $P < 0.01$). GWs differed from the other species in attacking prey from leaf undersides more frequently than any other substrate category.

The differences in substrate use were reduced when I compared all species on woodland edges (Fig. 4-5); RWs still used the greatest diversity of substrates (G for woodland edges = 62.46, df = 21, $P < 0.05$), but I found no significant difference in the proportional use of concealed vs. exposed substrates ($G = 0.19$, df = 3, $P > 0.05$) when wrens foraged in the same habitat.

Within species comparisons--prey substrates attacked in different seasons

Three species, HWs, PWs, and GWs, attacked a significantly greater proportion of prey on concealed substrates in the wet season than they did in the dry season (Fig. 4-6; G(HW) = 4.23, G(PW) = 8.49, G(RW) = 1.03, G(GW) = 12.16, df = 1, $P < 0.05$ for HWs, PWs, and GWs); consequently, I measured significantly greater diversity in prey substrate use for those species in the wet season (G(HW) = 42.82, G(PW) = 22.54, G(RW) = 9.00, G(GW) = 29.28, df = 8, $P < 0.05$ for HWs, PWs, and GWs). My sample sizes for RWs in the dry season were small, and although seasonal differences were statistically insignificant, they

Figure 4-6. Prey substrates attacked by four neotropical wrens in the wet and dry seasons. Substrate categories, abbreviations, and symbols are the same as for Figure 4-5. The numbers in parentheses in the lower left of each graph are the sample sizes. The numbers in the upper right corner of each graph are the normalized values of C(inv) and estimate relative diversity in use of prey substrates.


WET SEASON
DRY SEASON
GW
RW
PW
HW
C
E
.472
.756
.563
.734
.346
.347
.547
.561
(311)
(88)
(254)
(334)
(71)
(12)
(301)
(298)
PROPORTION
1.0
.5
0
2 3 4 5 6 7 8 9 10 ALL 2 3 4 5 6 7 8 9 10 ALL
PREY SUBSTRATE

suggest to me greater use of concealed substrates in the wet season as well (Fig. 4-6).

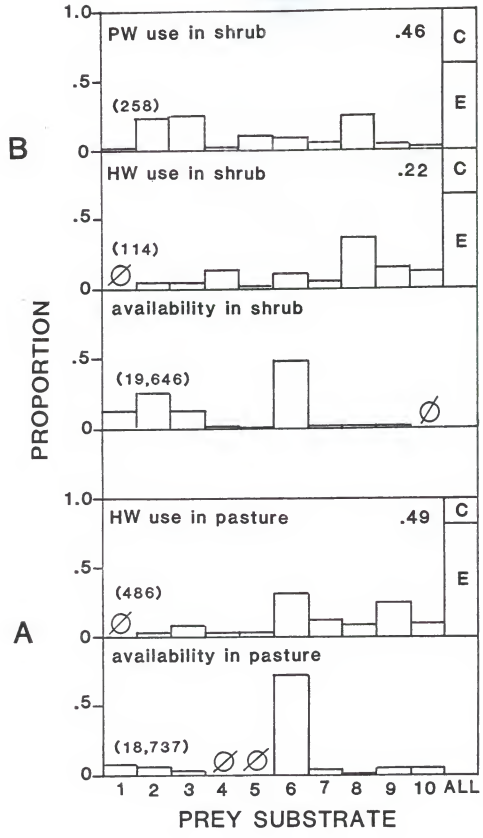
Within species comparisons--differences in prey substrate use among habitats and substrate use in relation to prey availability

I compared the proportional use of prey substrates by wrens in different habitats in relation to the proportional availability of prey on different substrates in those habitats (using data from Chapter III, I used the proportional similarity index (see Chapter Three, Methods) to estimate relative breadth in resource use based on prey substrates; a PS value of 1.0 represents the broadest possible niche.

HWs attacked significantly different prey substrates in pastures than they did in early successional shrub and edges (Figs. 4-7 a, b, and c; $G = 118.92$, $df = 16$, $P < 0.05$); in pastures they used abundant resources in short foliage near the ground, and they searched for rare prey in logpiles (Fig. 4-7a). HWs also foraged in logpiles in successional habitats, even though prey on those substrates were even less common than in pastures (Figs. 4-7 b and c). HWs ignored the increased abundance of prey on leaf surfaces in successional habitats, compared to pasture, but switched their behavior by concentrating on two new sources of rare prey in concealed substrates -- leaf bracts in successional shrub, and aerial leaf litter on woodland edges. Thus, HWs used the most specialilzed foraging behavior, due to greater use of concealed substrates ($G = 118.92$, $df = 8$, $P < 0.01$), in their secondary foraging habitats (Figs. 4-7 a, b and c).

PWs used similar substrates, but in significantly different proportions, when foraging in early successional shrub vs. edges (Figs. 4-7 b and c; $G = 72.23$, $df = 8$, $P < 0.05$); there was no difference in their proportional use of concealed vs. exposed substrates in the two

Figure 4-7. The proportional use of 10 prey substrates by wrens in relation to the proportional availability of prey by substrate. Histograms show the proportion of total attacks directed at prey on 10 different substrates: 1) air, 2) exposed foliage, 3) foliage undersides and stems, 4) leaf bracts and rolled leaves, 5) aerial leaf litter, 6) grass and herbaceous foliage, 7) ground litter, 8) twigs and branches, 9) logs, limbs and tree trunks, 10) woody crevices, ALL = all substrates combined. Histograms labelled E = exposed substrates (categories 1, 2, 6, 7, 8, and 9) and C = concealed substrates (categories 3, 4, 5, and 10) show the proportion of total attacks directed at prey on exposed vs. concealed substrates. The numbers in parentheses in the lower left of each graph are the sample sizes (the total number of arthropods > 5 mm or the total number of attacks). The numbers in the upper right of each graph are Proportional Similarity (PS) values and estimate the degree of overlap between distributions of availability and use (see text).


B
A
PROPORTION
1.0
.5
0
PW use in shrub
.46
C
E
(258)
HW use in shrub
.22
(114)
availability in shrub
(19,646)
HW use in pasture
.49
(486)
availability in pasture
(18,737)
1 2 3 4 5 6 7 8 9 10 ALL
PREY SUBSTRATE

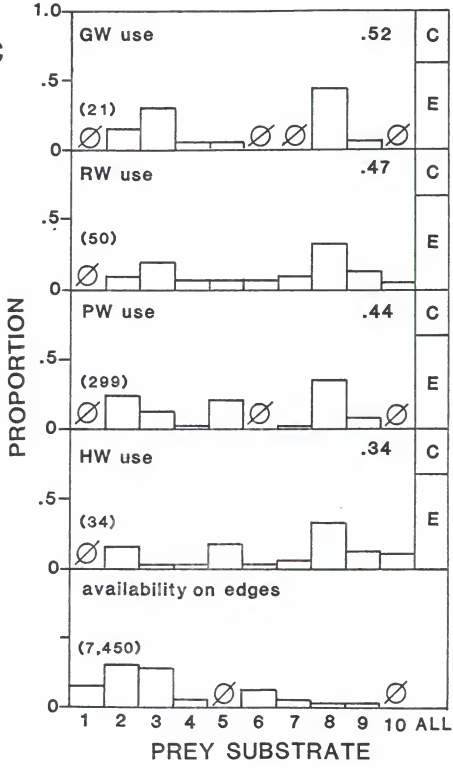


Figure 4-7 -- continued

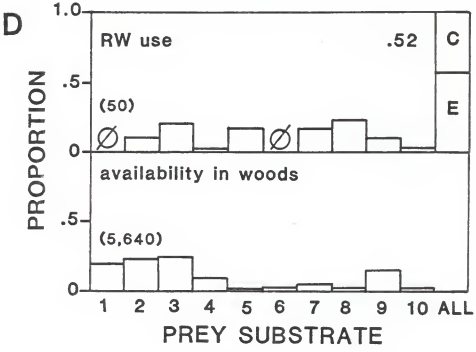


Figure 4-7 -- continued

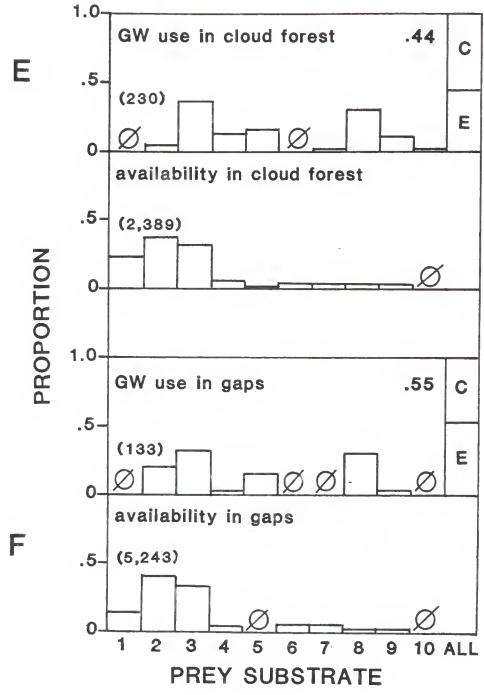


Figure 4-7 -- continued

habitats ($G = 0.69$, $df = 1$, $P > 0.05$), but PWs attacked rare prey in aerial leaf litter and on twigs more when on woodland edges than they did in shrub.

I found no significant difference in the use of prey substrates by RWs between woods and edges (Figs. 4-7 c and d; $G = 10.11$, $df = 8$, $P > 0.05$), and no difference in their use of concealed vs. exposed substrates in the two habitats ($G = 0.68$, $df = 1$, $P > 0.05$). RWs used relatively rare prey on woody surfaces in both habitats; they attacked prey on large woody surfaces and in the ground litter more than other species in the same habitat.

GWs attacked prey on a much greater diversity of substrates in cloud forest than they did in gaps; the distributions of substrate use were significantly different (Figs. 4-7 e and f; $G = 31.43$, $df = 8$, $P < 0.05$), although there was no difference in their proportional use of concealed vs. exposed substrates ($G = 2.52$, $df = 1$, $P > 0.05$). In both habitats, GWs specialized on leaf undersides, coincident with the high availability of prey there, and on rare prey on twigs and aerial leaf litter. GWs attacked prey on the same surfaces when on woodland edges (Fig. 4-7c).

On woodland edges, GWs used a lower diversity of substrates than the other wrens (Fig. 4-7c), but because they attacked more prey from substrates where arthropods were abundant, GWs had the greatest breadth in resource use. HWs, which used a greater proportion of rare prey substrates, had the least breadth in resource use (e.g. were the most specialized) in this habitat. HWs were also more specialized than PWs in early successional shrub, and PWs were more specialized than RWs on woodland edges.

Prey Types and Sizes

Comparisons among species--prey types

I found no significant difference in the frequency distributions of prey types captured in the field by HWs and PWs, although PWs captured a slightly greater diversity of prey types (Fig. 4-8; $G = 14.70$, $df = 9$, $P > 0.05$). Both species used a wide variety of arthropods, including Coleoptera, Orthoptera, and Lepidoptera. In addition, HWs commonly ate ants and PWs commonly ate hemipterans. I did not include RWs and GWs in this comparison because I could identify only a few of the items they captured in the field (see Fig. 4-8).

HWs, but not PWs, brought a significantly different distribution of prey types to their nests compared to what they caught in the field (Fig. 4-8; $G(HW) = 86.07$, $df = 9$, $P < 0.05$; $G(PW) = 12.90$, $df = 9$, $P > 0.05$). The distribution of prey types brought to nests differed significantly among the four wren species (Fig. 4-8; $G = 54.88$, $df = 21$, $P < 0.05$), even though no difference was apparent in prey captured in the field, at least between HWs and PWs. HWs brought only a few prey types, primarily lepidopteran larvae, orthopterans, and flying hymenoptera, to their young. HWs fed fewer beetles to their young than did the other wrens, and PWs brought proportionately more adult lepidoptera, and fewer larvae, than the other wrens. RWs and GWs brought a large proportion of larvae and beetles to their nests, but I identified only a few items they caught in the field, so a statistical comparison of the two distributions was not possible.

Comparisons among species--prey sizes

The size distributions of prey captured in the field were similar for all four wrens (Fig. 4-9; $G = 8.63$, 12 df, $p > 0.05$). Wrens

Figure 4-8. Frequency distributions of the types of prey caught by wrens in the field and brought to wren nests. Prey type categories are: 1) Arachnida, 2) adult Lepidoptera, 3) larvae, 4) Diptera, 5) flying Hymenoptera, 6) ants, 7) Homoptera, 8) Hemiptera, 9) Orthoptera, 10) Coleoptera. The numbers in parentheses in each graph are sample sizes. The numbers of each identified prey type caught in the field by RWs and GWs are given separately. The numbers in the upper right corner of each graph are the normalized values of C(inv) and estimate relative diversity in use of prey types.

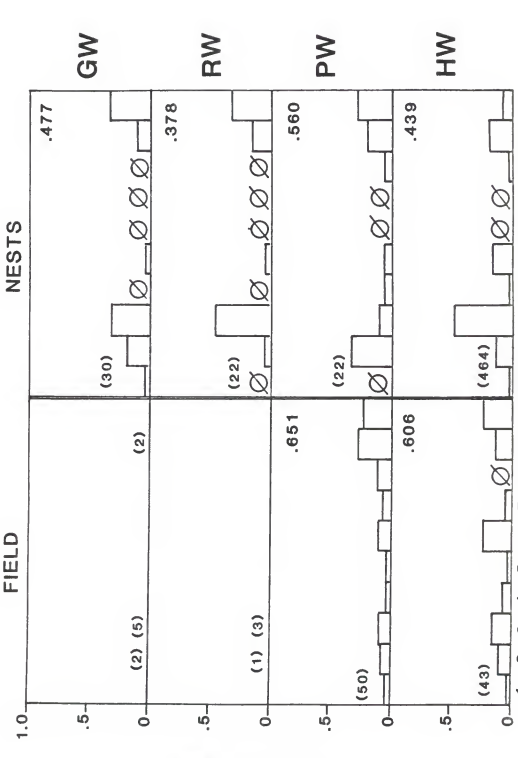
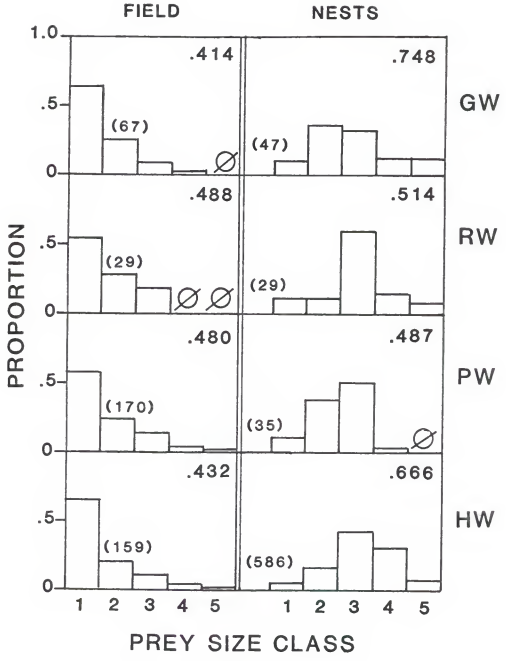

FIELD
NESTS
GW
RW
PW
HW
PROPORTION
1.0
.5
0
(2) (5)
(2)
(1) (3)
(50)
(43)
(30)
(22)
(22)
(464)
.477
.378
.560
.439
.651
.606
1 2 3 4 5 6 7 8 9 10 1 2 3 4 5 6 7 8 9
PREY TYPE

Figure 4-9. Frequency distributions of prey sizes caught by wrens in the field and prey sizes brought to wren nests. HW = House Wren, PW = Plain Wren, RW = Rufous-and-white Wren, GW = Gray-breasted Wood-Wren. Prey size classes are: 1) $\leq$ 5 mm, 2) 6 - 10 mm, 3) 11 - 20 mm, 4) 21 - 35 mm, and 5) 36 - 55 mm long. The numbers in parentheses in the lower left of each graph are sample sizes (total number of prey). The numbers in the upper right corner of each graph are normalized values of C(inv) and estimate relative diversity in use of prey size classes.


FIELD
NESTS
1.0
.5
0
.414
(67)
.748
(47)
GW
.488
(29)
.514
(29)
RW
.480
(170)
.487
(35)
PW
.432
(159)
.666
(586)
HW
PROPORTION
1 2 3 4 5
1 2 3 4 5
PREY SIZE CLASS

captured prey primarily in the smallest size class (less than 5 mm in length) and successively fewer prey in each larger class. All wrens brought significantly larger prey to their young compared to what they caught in the field (Figs. 4-9; G(HW) = 299.09, G(PW) = 39.08, G(RW) = 27.36, G(GW) = 48.53, df = 4, $P < 0.05$). The smallest species, HWs, showed the greatest difference in prey size distributions between the field and their nests; they brought a significantly larger distribution of prey to their nests than did any other wrens (G = 50.01; df = 12, $P < 0.05$).

Aviary Experiments

Overall, wrens in a controlled aviary habitat performed similarly, as estimated by their success at finding prey. The results were strongly influenced by small sample sizes, however, because variance among individuals within a species was often as great as variance among species.

Experiment I--foraging in a controlled habitat

I compared foraging speed of wrens on four different substrates in the aviary--ground litter, logs, woody tangle, and foliage more than 1 m high, and found that all species moved faster when on ground litter or logs compared to foliage or twigs above ground (Table 4-8). Regardless of the substrate, however, the smaller species, HWs and GWs, moved faster than PWs and RWs (Table 4-8). This was consistent with the differences in foraging speed I measured among species in the field.

I did not compare attack techniques in the aviary because these were directly determined by the placement of prey; all wrens used similar methods of obtaining the same prey items.

Table 4-8. Foraging speeds of wrens on different aviary substrates.

	perches/sec, (n)[a]				
	HW	PW	RW	GW	H
ground litter	0.67 (12)	0.34 (5)	0.30 (27)	0.48 (23)	11.33[b]
logs	0.50 (13)	0.26 (23)	0.30 (39)	0.40 (23)	22.27[b]
twig tangle	0.33 (20)	0.24 (30)	0.19 (19)	0.36 (8)	16.19[b]
leafy foliage	0.37 (32)	0.29 (55)	0.24 (28)	0.39 (23)	19.84[b]

[a] n = the number of 10-perch sequences used to calculate mean foraging speed.

[b] All nonparametric Kruskal-Wallis tests (H) significant at $P < 0.05$ with 3 df.

None of the three estimates of foraging success--number of prey captured, capture rate, or average time between prey captures--differed significantly among species, although there was a consistent trend for RWs, and secondarily, GWs, to find more prey at more frequent intervals (Table 4-9). The variances in individual capture rates within species were high, but homogeneous across species (F(max) Test; X^2 = 12.08, df = 4,2, $P > 0.05$).

Out of a maximum of 40% concealed prey items, GWs, on average, found the most (33%) and HWs found the least (21%), but these differences were not statistically significant (Table 4-9). Again, the pattern was consistent with my results indicating that GWs found more prey on concealed substrates in the field than did the other wrens.

I calculated overlap (PS) between the proportional use of prey on nine different substrates and the proportional prey availability to estimate relative breadth in resource use. Here, proportional prey availability on different substrates was fixed and equal (0.11). As in my field estimates, PS values (thus foraging breadth) of the two forest wrens, RWs and GWs, averaged greater than the foraging breadth of the open habitat wrens (Fig. 4-10; Table 4-9), although the differences among species in the aviary were statistically insignificant. The slightly greater foraging breadth of RWs and GWs may have contributed to their slightly greater capture rates.

Experiment II--response to changes in prey substrate

In a separate analysis for each substrate trial, I found no significant differences among species in the four estimates of success, regardless of the prey substrate. I then pooled results from all four trials to obtain an overall species mean for each of three estimates of

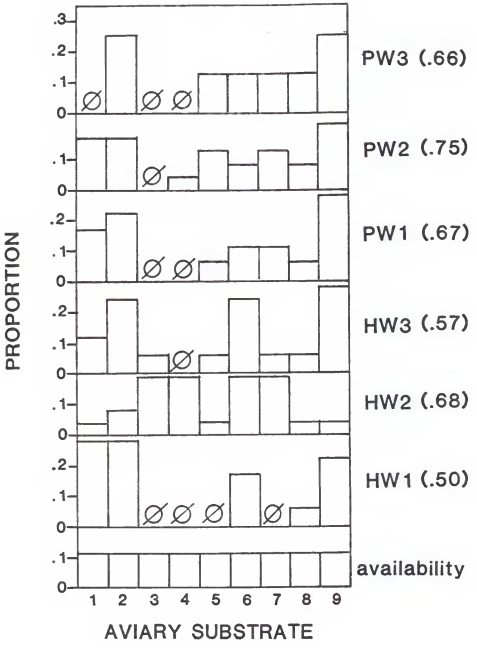
Table 4-9. Foraging success and use of prey substrates by wrens in an aviary habitat.

	Wren Species				
	HW	PW	RW	GW	H
Number of individuals	3	3	4	3	
Mean number of prey captured	20.3	19.3	24.5	22.0	2.66[a]
Capture rate (n/min)	0.21	0.17	0.25	0.24	6.43[a]
Average time (mins) between prey captures	5.4	5.3	3.7	4.4	5.56[a]
Mean proportion of concealed prey	0.21	0.30	0.26	0.33	1.75[a]
Mean PS[b] between prey substrates used and availability	0.58	0.69	0.75	0.75	5.98[a]

[a]All Kruskal-Wallis tests insignificant with 3 df and $P > 0.05$.

[b]PS = Proportional Similarity.

Figure 4-10. The proportional use of nine prey substrates by wrens in relation to prey availability in an aviary. Histograms show the proportion of each wren's total attacks directed at prey on the following nine substrates: 1) leaf tops and undersides more than 1 m high, 2) twigs and branches (any height), 3) ground litter, 4) leaf tops and undersides less than 10 cm high, 5) leaf bracts less than 1 m high, 6) exposed woody surfaces (any height), 7) concealed woody crevices (any height), 8) aerial leaf litter more than 1 m high, and 9) suspended in the air on monofilament fishing line. The bottom histogram shows the proportional availability of mealworms on those substrates. The numbers in parentheses following each wren's identification are Proportional Similarity values and estimate overlap in availability and use.


PROPORTION
.3
.2
.1
0
PW3 (.66)
PW2 (.75)
PW1 (.67)
HW3 (.57)
HW2 (.68)
HW1 (.50)
availability
1 2 3 4 5 6 7 8 9
AVIARY SUBSTRATE

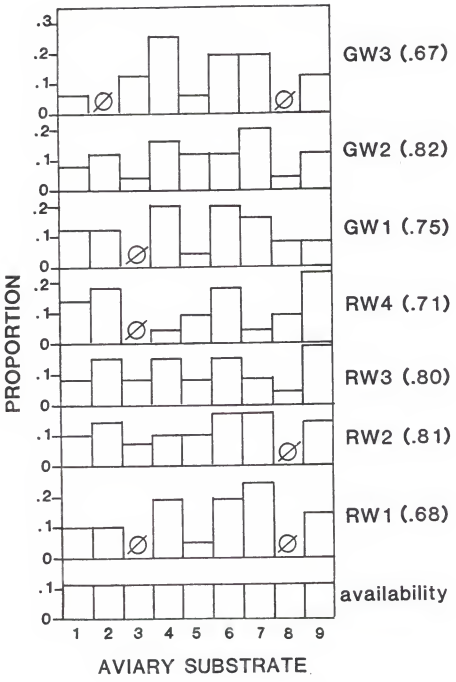


Figure 4-10 -- continued

foraging success; none of these estimates were significantly different among the four wren species (Table 4-10). Although foraging success was dependent on the prey substrate (all species scored highest on logs and worst when mealworms were hidden in ground litter), this experiment provided no evidence that some species were better able to cue into short-term changes in prey location than others.

Experiment III--response to a novel foraging microhabitat

I found no significant difference among species in any of the four measures of their response to a novel prey substrate -- total number captured, capture rate, time required to find the first prey, and average time between prey captures (Table 4-11). The high variance among individuals within species was particularly apparent in estimates of the time required to find the first prey item (Table 4-11).

Discussion and Synthesis

Discussion

My results provide no evidence for my initial hypothesis that wrens in open, disturbed habitats have more flexible foraging behavior than forest wrens. I did not find a single pattern associating higher reproductive effort with greater foraging flexibility among species in disturbed habitats. In most measures, I found greater foraging variability among forest wrens. My results are consistent, however, with results from Chapter III showing that forest wrens, not open habitat wrens, should have encountered the greatest variation in their arthropod food supply, and should have had the greatest diffficulty finding relatively scarce and concealed forest arthropods that were dispersed over a wide variety of substrates.

Table 4-10. Estimates of foraging success among wrens subjected to changes in prey substrates.

	Wren Species				
	HW	PW	RW	GW	H
Pooled number of trials	12	12	16	12	
Capture rate (n/min)	0.13	0.16	0.15	0.16	2.02[a]
Mean time (mins) to capture first prey	8.2	10.1	11.7	9.0	4.29[a]
Mean time (mins) between prey captures	5.9	6.9	4.9	4.7	1.41[a]

[a]All Kruskal-Wallis nonparametric ANOVA tests insignificant with 3 df and $P > 0.05$.

Table 4-11. Estimates of foraging success among wrens encountering a novel foraging substrate.

	Wren Species				
	HW	PW	RW	GW	H
Number of individuals	3	3	4	3	
Mean number of prey captured	6.0	4.7	5.8	5.3	0.80[a]
Capture rate (n/min)	0.08	0.07	0.08	0.06	1.01[a]
Mean time (mins) to capture first prey	14.3	2.0	3.0	19.3	0.83[a]
Mean time (mins) between prey captures	9.4	9.0	9.3	9.2	0.05[a]

[a]All Kruskal-Wallis tests insignificant with 3 df and $P > 0.05$.

Open-habitat HWs had high variability in some foraging parameters compared to other wrens, including their use of foraging positions, and they used very different prey substrates in different habitats. But the other open-habitat species, PWs, were the least variable of the wrens in several foraging parameters, and were considerably less flexible than HWs in the same habitats. In particular, PWs used restricted foraging positions on woodland edges where they systematically searched aerial leaf litter, a behavior that has been reported for a variety of tropical birds, including other wrens in the genus Thryothorus (Gradwohl and Greenberg 1982, Remsen and Parker 1984). On edges, I measured low variance in PW behavior because they concentrated on a single substrate for long periods.

The two forest wrens, RWs and GWs, had the greatest variability in most measures of foraging behavior. I measured greater breadth in attack techniques used by RWs and GWs; they relied more heavily than did HWs and PWs on techniques used to capture prey at greater distances or in concealed substrates--pouncing, hanging and flipping leaves. RWs and GWs also used the greatest diversity of foraging positions, the broadest variety of prey substrates, and the greatest proportion of concealed substrates. This was consistent with the high proportion of prey in concealed substrates and the low food availability in their habitats. Results from the aviary experiments were consistent with the differences I measured in the field, but statistically insignificant.

GWs, in particular, attacked prey in concealed substrates more than the other wrens, and they were the most generalized foragers in their use of prey substrates in relation to prey availability, primarily because they used leaf undersides to a greater extent than other wrens.

Leaf undersides were particularly important to GWs in the wet cloud forest and during the wet season when prey accumulated on more protected surfaces. Greenberg and Gradwohl (1980) found that 70-80% of the total understory arthropods in a tropical lowland forest occurred on leaf undersides, and they found several species of birds that specialized on this substrate.

My results suggest that different aspects of foraging behavior were dependent on morphology and on the habitat--either on structural differences in the dispersion and types of perches and/or on differences in the abundance and dispersion of prey. Habitat structure is known to influence several aspects of behavior including foraging maneuvers, choice of foraging position, and foraging speed (Alerstam and Ulfstrand 1977, Maurier and Whitmore 1981, Robinson and Holmes 1982, 1984). I measured changes in these parameters among habitats also, but my results indicate that prey availability, and secondarily, wren size, were more important determinants of foraging behavior than physical features of the habitat.

Foraging speed, attack rates, and rates of change in foraging position were apparently partially dependent on the size of the wren, or at least, on morphological characteristics correlated with wren size in these four species. The smallest wrens moved faster, attacked prey more often, and changed foraging positions more often than the larger wrens. Fitzpatrick (1980) found a similar relationship between bird size and speed among New World flycatchers (F. Tyrannidae), while Robinson and Holmes (1982) found that attack rates were correlated with foraging speed among a variety of temperate insectivorous birds. My aviary experiments demonstrated that, whereas foraging speed was determined

partly by perch substrate, the same differences in speed occurred among species even on the same aviary substrates, as well as when wrens foraged in the same habitat in the field.

In contrast, capture rates were not necessarily correlated with foraging speed, or even with attack rates. In several comparisons, I found differences in attack rates between seasons or habitats, but capture rates rarely differed significantly in the same comparisons. The lack of correlation between attack and capture rates suggests that 1) either significant changes in foraging behavior did not influence capture rates appreciably or, 2) significant changes in foraging behavior were necessary to maintain a similar level of food intake in habitats differing in prey availability. For example, variable foraging behavior by GWs in cloud forest may have been necessary to achieve the same capture rate that they achieved in gaps, where prey were more abundant, and where diverse behavior was not required to maintain a given intake level.

Prey availability differed markedly among habitats, and my results suggest that this was an important factor determining foraging behavior. First, comparisons among wren species in the same habitat, woodland edge, reduced (but did not eliminate) differences in foraging speed, capture rates, and diversity in techniques and prey substrates used. The differences in these parameters were statistically insignificant when I compared species in the aviary with an identical habitat structure and prey distribution. Capture rates of different species were nearly equal in the aviary, suggesting that capture rate, as well, depended primarily on the characteristics of prey availability and location.

Second, the most striking within-species differences in foraging behavior and capture rates occurred among GWs, the only species that foraged in both high and lower elevation habitats. In low elevation woods and edges, GWs used a lower diversity of techniques, foraging positions, and prey substrates compared to what they used in cloud forest and gaps. Although this difference could have resulted primarily from the smaller sample sizes at lower elevations, capture rates, less influenced by sample size than diversity estimates, were only one-third what they were in cloud forest and gaps, despite equivalent attack rates at both elevations. This suggests that either GWs were less efficient at capturing prey at lower elevations, or that they caught a much greater proportion of very small prey items that I did not detect. In either case, their intake rate of biomass was less at lower elevations. The woods where I gathered these data lie at the lower elevational limit of this species at Monteverde (1300 m). GWs foraging in low elevation woods would have encountered an entirely different prey distribution, habitat structure, and bird community from that encountered in cloud forest. Capture rates and the behavioral variability of GWs may have declined if they were unable to adjust to differences such as the lower food availability and/or to increased interference by competing insectivorous species. In addition to RWs foraging in the same habitat, GWs would have encountered congeneric White-breasted Wood-Wrens in low elevation woods. Differences in habitat structure were probably not an important factor determining lower capture rates of GWs at lower elevations because GWs foraging in a woodland edge aviary had capture rates equivalent to other wrens. Unlike the situation in natural

woodland edges, however, prey availability in the aviary was relatively high, and there were no competitors.

GWs also were the only species to show consistent behavioral differences between two primary foraging habitats, cloud forest and gaps. GWs used a greater diversity of foraging positions, techniques, and prey substrates in cloud forest, where prey were less abundant and distributed over a wider variety of substrates than they were in gaps.

I observed some seasonal changes in foraging parameters for all wrens, but changes in any one species were no more pronounced or predictable than in any others. RWs, in the habitat with the most seasonal food supply, attacked prey much less frequently during the dry season, when prey were relatively scarce. All wren species had lower capture rates during the dry season, and the magnitude of this difference was greatest for RWs, but none of the seasonal differences were statistically significant. In general, wrens foraged slower, changed foraging position more often, attacked prey more often, and used a greater diversity of foraging positions during the dry season, when food was less available in most habitats, than they did in the wet season. These changes suggest that wrens increased their intensity and thoroughness of searching when prey availability decreased (see also Root 1967, Greenberg 1984b). At the same time, wrens generally attacked prey from a lower diversity of substrates, and from a higher proportion of exposed substrates, during the dry season, indicating changes in the locations where prey were found. Several factors may have contributed to this shift. First, hemipterans and flying hymenopterans peaked during the dry season in open habitats, and I found these insects primarily on exposed substrates. Second, in the wettest habitats, and

during wet weather in all habitats, I found that insects moved from exposed surfaces (e.g. leaf tops) to more protected, and therefore more concealed, surfaces (e.g. leaf undersides, bracts, etc.; but see Greenberg and Gradwohl 1980). Finally, wrens may have increased their use of some concealed substrates (e.g. leaf undersides and rolled leaves) when highly desirable prey, such as lepidopteran larvae, became seasonally abundant there in the wet season (see Fig. 3-5c).

Unlike the other wrens, GWs used a greater diversity of foraging positions and techniques during the wet season, as compared with the dry season. This result could refer to their greater use of concealed prey substrates during the wet season. The wet season also includes most of the months from June through February when GWs are most likely to join mixed foraging flocks (Powell 1979, Shopland 1985, pers. observ.). GWs may use a greater diversity of foraging behaviors when in flocks, as do other mixed-flock participants (Krebs 1973, Shopland 1985).

Wrens at Monteverde showed increased selectivity of prey types and sizes brought to their young compared to items caught in the field, as has been described for many other birds (Tinbergen 1960, Lind 1965, Verner 1965, Royama 1966, 1970, Root 1967, Hartwick 1976, Biermann and Sealy 1982). Orians and Pearson (1979) hypothesized that birds should bring larger, more profitable prey to their nests to reduce the number of trips and the energetic cost of feeding young. At Monteverde, HWs showed the greatest specialization in the prey items brought to their young. Although I found no significant differences in prey distributions caught by wrens in the field, HWs brought a significantly larger size distribution of prey to their young, despite the much smaller size of HWs compared to the other species. Forty-seven percent

of the items brought to HW nests were large, soft-bodied lepidopteran larvae. These results are consistent with optimal foraging theory, which predicts greater specialization in prey choice where food resources are less limiting (Schoener 1971, MacArthur 1972, Werner and Hall 1974, Krebs 1978, Morse 1980).

Synthesis

Wrens in both high and low elevation forests are the most severely food-limited of the four species I studied. Their habitats probably do not provide the potential for a high reproductive effort or a long breeding season. Forest wrens may be more constrained than open-habitat wrens in timing their breeding to coincide with peak arthropod abundance. Additionally, they may be more limited in the number of offspring they can produce by lower food levels. Other studies have suggested that tropical forest insectivores are severely constrained in their reproduction by food limitation and by the difficulty of finding arthropods (Gradwohl and Greenberg 1982, Marcotullio and Gill 1985). At the same time, where food is difficult to find, a longer period of parental care, which usually precludes further reproduction, may be necessary, compared to habitats where food is plentiful. Morse (1980) suggested that heavy reliance on learned behavior patterns should improve the capabililty of animals to respond to variable conditions, and longer periods of parental care presumably extend the time available for observational learning (see Alcock 1969, Krebs et al. 1972, Morse 1980). Fogden (1972) found that insectivorous birds in tropical forests of Sarawak were fed by their parents for 6-7 months after fledging and related this to their need to learn how to recognize and find highly cryptic prey. Other authors have suggested that the difficulty of

foraging technique should correlate positively with the length of parental care (Davies 1976, Davies and Green 1976, Morse 1980). In this study, higher variance in reproductive success of forest wrens would be expected, due to higher rates of predation in their habitat, and higher rates of desertion and starvation should occur due to the less predictable food supply. For example, some birds incubate less constantly when food availabililty is low, and greater nest mortality may result (Bryant 1975, Murray et al. 1980). Facultative re-nesting, which I observed among RWs in the most variable habitat, should occur under conditions leading to variable reproductive success.

Wrens in the open habitats were much less food-limited than wrens in forests. The continuously higher biomass of important food types provided the potential for a higher reproductive rate and a longer breeding season. Apparently, however, only HWs, and not PWs, capitalized on this potential to a great degree. Here, behavioral flexibility was associated with a higher reproductive rate, given the potential offered by high and constant food availability in the habitat. HWs had greater behavioral flexibility than PWs in nearly all measures, even when they foraged in the same habitats. Why don't PWs exploit open habitats in a manner similar to that of HWs, in order to increase their reproductive output? Several possible explanations deserve further study. First, multiple brooding may be more common among PWs than indicated by the single case I observed in a small sample; thus, PWs might have a higher average reproductive output than suggested from this study. Second, PWs use shrub and edge habitats to a much greater degree than HWs, and food may be harder to find there, compared to the very open areas used primarily by HWs. Third, nest site selection differed

markedly between the two species; HWs selected less vulnerable sites, so that the expected nesting success was lower among PWs. PWs may expend smaller reproductive effort/time in response to variability in their expected reproductive success. Finally, HWs may possess flexible behavior characteristics not shared by PWs. Further experimental work is needed to determine the importance of this last factor because, whereas my aviary experiments indicated that PWs foraged less efficiently in a controlled habitat, small sample sizes precluded statistical significance in the differences.

The most striking difference in the way wrens exploited their food supplies was in the distribution of prey brought to young. Where food was predictably abundant, HWs could afford to be more particular in what they fed their young. HWs brought the greatest proportion of larger, more easily digested larvae (Biermann and Sealy 1982) to their chicks, even though I sampled greater numbers of larvae in edge and forest habitats where HWs seldom foraged (Fig. 3-5c). Chicks fed a higher proportion of large, soft-bodied prey may grow faster and/or fledge at higher relative weights (Von Brömssen and Jansson 1980); this, in turn, may enhance the reproductive success of their parents, and it minimizes the length of the nesting cycle, thereby enhancing the opportunity for the parents to raise subsequent broods. Due to lower predation rates and higher food availability year-round, the probability of success in re-nesting is nearly always high for HWs.

The results of my study then, indicate that behavioral flexibility is important in two ways. It acts both as a mechanism to capitalize on a potentially productive environment, and as a mechanism to exploit a variable, less favorable habitat where prey are more difficult to find.

APPENDIX

SUPPLEMENTARY TABLES USED IN ANALYSIS OF ARTHROPOD DATA

Table A-1. Coefficients of variation (%) in biomass among four adjacent transects, averaged over all sites within each habitat.

	Habitat[a]					
Sample period[b]	1	2	3	4	5	6
1	70	81	58	111	62	58
2	81	55	67	39	115	120
3	53	46	83	57	127	112
4	54	45	58	73	69	116
5	49	37	88	100	89	60
6	70	67	92	91	69	72
7	59	56	58	91	97	72
8	65	56	56	57	68	80
9	63	52	47	88	107	44
10	52	65	70	84	73	69
11	28	42	36	60	67	52
12	23	72	96	81	106	109
13	47	52	54	64	58	73
14	20	56	56	39	77	36
15	60	46	58	62	53	35
16	37	51	68	57	31	42
17	29	30	60	86	27	42

[a]Habitat numbers correspond to those given in Chapter III, Methods: 1) pasture, 2) early successional shrub, 3) low elevation woodland edge, 4) cloud forest gap, 5) low elevation woods, and 6) cloud forest.

[b]See Chapter III, Methods for dates of sample periods.
I computed means for four sites/habitat in sample periods 1 through 10, and for three sites/habitat in sample periods 11 through 17.
Kendall coefficient of concordance (Siegel 1956), $W = .3042$, $X^2 = 29.20$, $df = 16$, $P < .05$.

Table A-2. The dominance concentration, C(inv), averaged over all transects within each habitat.

Sample period[b]	Habitat[a] 1	2	3	4	5	6
1	3.85	3.12	2.52	2.92	2.06	2.62
2	3.05	3.30	3.07	3.46	1.60	2.15
3	3.54	3.68	2.54	3.06	1.93	1.88
4	2.99	4.03	3.31	3.52	2.16	3.04
5	2.64	3.47	2.77	2.69	2.29	2.27
6	3.01	3.08	2.54	2.26	1.93	2.60
7	3.45	2.93	2.95	2.92	2.19	3.35
8	4.04	3.11	3.12	3.61	3.07	3.06
9	3.23	3.74	3.12	3.13	2.07	3.10
10	3.75	3.76	3.47	3.12	2.19	2.97
11	3.75	3.93	2.95	2.42	2.52	3.08
12	4.23	3.20	2.69	2.92	1.73	2.49
13	3.31	3.98	2.25	2.66	2.61	2.54
14	4.23	3.18	3.13	3.14	2.95	2.73
15	3.92	3.26	3.01	3.62	2.31	3.15
16	3.20	3.52	3.45	2.98	3.25	3.05
17	3.15	3.82	2.66	2.75	3.36	2.31

[a]Habitat numbers are the same as for Table A-1.

[b]See Chapter III, Methods for dates of sample periods.
Averages were computed over 16 transects for sample periods 1 through 10 and over 12 transects for sample periods 11 through 17.
Kruskal-Wallis $H = 47.14$, $df = 5$, $P < .001$.

Table A-3. The proportional similarity (PS) of arthropod groups between transects, averaged over all pair-wise combinations within sites.

Sample Period[b]	Habitat[a] 1	2	3	4	5	6
1	0.417	0.391	0.417	0.444	0.573	0.400
2	0.392	0.452	0.413	0.498	0.290	0.264
3	0.485	0.545	0.353	0.510	0.256	0.406
4	0.484	0.649	0.516	0.555	0.404	0.539
5	0.541	0.544	0.500	0.646	0.510	0.479
6	0.582	0.576	0.354	0.606	0.508	0.548
7	0.495	0.542	0.430	0.462	0.372	0.618
8	0.476	0.627	0.488	0.547	0.376	0.475
9	0.486	0.616	0.459	0.447	0.549	0.421
10	0.530	0.544	0.488	0.482	0.564	0.542
11	0.601	0.650	0.582	0.538	0.470	0.659
12	0.712	0.525	0.368	0.527	0.394	0.699
13	0.665	0.708	0.354	0.653	0.395	0.571
14	0.728	0.558	0.532	0.739	0.646	0.607
15	0.614	0.629	0.499	0.542	0.511	0.583
16	0.773	0.651	0.402	0.576	0.492	0.539
17	0.673	0.636	0.431	0.589	0.556	0.446

[a]Habitat numbers are the same as for Table A-1.

[b]See Chapter III, Methods for dates of sample periods.
PS values were averaged over 24 adjacent pairs of transects for periods 1 through 10, and over 18 transect pairs for periods 11 through 17.
Kruskal-Wallis $H = 23.64$, $df = 5$, $P < .05$.

Table A-4. The proportion of arthropods (greater than 5 mm in length) found in or on concealed substrates.

	Habitat[a]					
Sample Period[b]	1	2	3	4	5	6
1	0.024	0.141	0.220	0.255	0.150	0.308
2	0.053	0.189	0.470	0.357	0.712	0.596
3	0.067	0.132	0.361	0.305	0.546	0.650
4	0.026	0.178	0.333	0.534	0.568	0.558
5	0.007	0.133	0.228	0.348	0.700	0.432
6	0.022	0.191	0.377	0.456	0.709	0.643
7	0.046	0.169	0.323	0.495	0.463	0.368
8	0.031	0.163	0.397	0.442	0.375	0.366
9	0.050	0.166	0.306	0.506	0.256	0.393
10	0.159	0.156	0.316	0.384	0.360	0.410
11	0.020	0.114	0.474	0.520	0.229	0.417
12	0.022	0.060	0.329	0.328	0.333	0.413
13	0.012	0.066	0.105	0.321	0.391	0.241
14	0.016	0.126	0.586	0.456	0.394	0.310
15	0.042	0.111	0.317	0.421	0.390	0.215
16	0.025	0.135	0.320	0.485	0.331	0.372
17	0.035	0.161	0.398	0.551	0.327	0.500

[a]Habitat numbers are the same as for Table A-1.

[b]See Chapter III, Methods for dates of sample periods.
Kruskal-Wallis $H = 69.72$, $df = 5$, $P < 0.05$.

LITERATURE CITED

Abbott, I., L. K. Abbott, and P. R. Grant. 1977. Comparative ecology of Galapagos ground finches (Geospiza Gould): Evaluation of the importance of floristic diversity and interspecific competition. Ecological Monographs 47: 151-184.

Airola, D. A. and R. H. Barrett. 1985. Foraging and habitat relationships of insect-gleaning birds in a Sierra Nevada mixed conifer forest. Condor 87: 205-216.

Alcock, J. 1969. Observational learning in birds. Ibis 111: 308-321.

Alerstam, T. and S. Ulfstrand. 1977. Niches of tits (Parus spp.) in two types of African woodland. Ibis 119: 521-524.

Altmann, J. 1974. Observational study of behaviour: sampling methods. Behaviour 49: 227-267.

Alvarez-López, H., M. D. Heredia-Flores, and M. C. Hernández-Pizarro. 1984. Reproduccion del cucarachero común (Troglodytes aedon, Aves, Troglodytidae) en el Valle del Cauca. Caldasia 14: 85-123.

American Ornithologists' Union. 1983. Check-list of North American Birds. Sixth edition. American Ornithologists' Union, Washington D. C., USA.

Anderson, T. R. 1977. Reproductive responses of sparrows to a superabundant food supply. Condor 79: 205-208.

Armstrong, E. A. 1955. The wren. Collins, London, England.

_____ and H. L. K. Whitehouse. 1977. Behavioural adaptations of the Wren (Troglodytes troglodytes). Biological Review 52: 235-294.

Arnold, K. A. 1966. The avian genus Thryothorus (Troglodytidae) in Costa Rica: a study in species diversity. Ph.D. Dissertation. Louisiana State University, Lafayette, Louisiana.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103: 458-473.

Askins, R. A. 1983. Foraging ecology of temperate-zone and tropical woodpeckers. Ecology 64: 945-956.

Bechard, M. J. 1983. Food supply and the occurrence of brood reduction in Swainson's Hawk. Wilson Bulletin 95: 233-242.

Biermann, G. C. and S. G. Sealy. 1982. Parental feeding of nestling Yellow Warblers in relation to brood size and prey availability. Auk 99: 332-341.

Blake, J. G. and W. G. Hoppes. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. Auk 103: 328-340.

Brewer, R. and L. Swander. 1977. Life history factors affecting the intrinsic rate of natural increase of birds of the deciduous forest biome. Wilson Bulletin 89: 211-232.

Brown, J. L. 1978. Avian communal breeding systems. Annual Review of Ecology and Systematics 9: 239-262.

_____, E. R. Brown, S. D. Brown, and D. D. Dow. 1982. Helpers: effects of experimental removal on reproductive success. Science 215: 421-422.

Bryant, D. M. 1975. Breeding biology of House Martins Delichon urbica in relation to aerial insect abundance. Ibis 117: 180-216.

Burley, N. 1980. Clutch overlap and clutch size; alternative and complementary reproductive tactics. American Naturalist 115: 223-246.

Buskirk, W. A. and R. Buskirk. 1976. Changes in arthropod abundance in a highland Costa Rican forest. American Midland Naturalist 95: 288-298.

Carriker, M. A., Jr. 1910. An annotated list of the birds of Costa Rica including Cocos Island. Annals of the Carnegie Museum 6: 314-915.

Clark, A. B. and D. S. Wilson. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. Quarterly Review of Biology 56: 253-277.

Cody, M. L. 1966. A general theory of clutch size. Evolution 20: 174-184.

_____. 1971. Ecological aspects of reproduction. Pages 461-512 in D. S. Farner and J. R. King, editors. Avian Biology, Volume I. Academic Press, New York, New York, USA.

Colwell, R. K. and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567-576.

Cox, D. R. and P. A. W. Lewis. 1966. The statistical analysis of series of events. John Wiley and Sons, New York, New York, USA.

Davies, N. B. 1976. Parental care and the transistion to independent feeding in the young spotted flycatcher (Muscicapa striata). Behaviour 59: 280-295.

_____ and R. E. Green. 1976. The development and ecological significance of feeding techniques in the reed warbler (Acrocephalus scirpaceus). Animal Behaviour 24: 213-229.

Diamond, J. M. 1975. Assembly of species communities. Pages 342-444 in M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts, USA.

Dobzhansky, T. H. 1950. Evolution in the tropics. American Scientist 38: 209-221.

Dunn, E. K. 1972. Effect of age on the fishing ability of sandwich terns Sterna sandvicensis. Ibis 114: 360-366.

Ebenman, B. and S. G. Nilsson. 1982. Components of niche width in a territorial bird species: habitat utilization in males and females of the Chaffinch (Fringilla coelebs) on islands and mainland. American Naturalist 119: 331-344.

Emlen, S. T. 1978. The evolution of cooperative breeding in birds. Pages 245-281 in J. R. Krebs and N. B. Davies, editors. Behavioural Ecology: an evolutionary approach. Blackwell Publishers, Oxford, England.

Feinsinger, P. 1976. Organization of a tropical guild of nectarivorous birds. Ecological Monographs 46: 257-291.

_____, E. E. Spears, and R. W. Poole. 1981. A simple measure of niche breadth. Ecology 62: 27-32.

Findlay, C. S. and F. Cooke. 1983. Genetic and environmental componenets of clutch size variance in a wild population of Lesser Snow Geese (Anser caerulescens). Evolution 37: 724-734.

Fitzpatrick, J. W. 1980. Foraging behavior of neotropical tyrant flycatchers. Condor 82: 43-57.

Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114: 307-342.

Garson, P. J. 1980. Male behaviour and female choice: mate selection in the wren. Animal Behaviour 28: 491-502.

Gradwohl, J. and R. Greenberg. 1982. The effect of a single species of avian predator on the arthropods of aerial leaf litter. Ecology 63: 581-583.

Greenberg, R. 1983. The role of neophobia in determining the degree of foraging specialization in some migrant warblers. American Naturalist 122: 444-453.

_____. 1984a. Neophobia in the foraging-site selection of a neotropical migrant bird: an experimental study. Proceedings of the National Academy of Science USA 81: 3778-3780.

_____. 1984b. The winter exploitation system of Bay-breasted and Chestnut-sided Warblers in Panama. University of California Publications in Zoology 116: 1-107.

_____ and J. Gradwohl. 1980. Leaf surface specializations of birds and arthropods in a Panamanian forest. Oecologia 46: 115-124.

Hagan, J. M. 1986. Temporal patterns in pre-fledgling survival and brood reduction in an Osprey colony. Condor 88: 200-205.

Hardy, J. W. 1976. Comparative breeding behavior and ecology of the Bushy-crested and Nelson San Blas Jays. Wilson Bulletin 88: 96-120.

Hartwick, E. B. 1976. Foraging strategy of the Black Oyster Catcher (Haematopus bachmani Audubon). Canadian Journal of Zoology 54: 142-155.

Haverschmidt, F. 1952. Nesting behavior of the Southern House Wren in Surinam. Condor 54: 292-295.

Higuchi, H. and H. Momose. 1981. Deferred independence and prolonged infantile behaviour in young Varied Tits, Parus varius, of an island population. Animal Behaviour 29: 523-528.

Hogstedt, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. Science 210: 1148-1150.

Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center, San José, Costa Rica.

Horn, H. S. 1978. Optimal tactics of reproduction and life history. Pages 411-429 in J. R. Krebs and N. B. Davies, editors. Behavioural ecology: an evolutionary approach. Blackwell Publishers, Oxford, England.

Howe, H. F. 1976. Egg size, hatching asynchrony, sex, and brood reduction in the Common Grackle. Ecology 57: 1195-1207.

Janzen, D. H. 1969. Birds and the ant x acacia interaction in Central America, with notes on birds and other myrmecophytes. Condor 71: 240-56.

_____. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54: 687-708.

_____ and T. W. Schoener. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. Ecology 49: 96-110.

Kale, H. W., II. 1965. Ecology and bioenergetics of the Long-billed Marsh Wren, Telmatodytes palustris griseus (Brewster), in Georgia salt marshes. Publications of the Nuttall Ornithological Club 5: 1-142.

Keast, J. A. and A. J. Marshall. 1954. The influence of drought and rainfall on reproduction in Australian desert birds. Proceedings of the Zoological Society of London 124: 493-499.

Kendeigh, S. C. 1941. Territorial and mating behavior of the House Wren. Illinois Biological Monographs 18: 1-120.

_____. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Ontario Department of Lands and Forests Bulletin 1: 1-100.

Kluyver, H. N., J. H. vanBalen, and A. J. Cave. 1977. The occurrence of time-saving mechanisms in the breeding biology of the Great Tit, Parus major. Pages 153 - 169 in B. Stonehouse and C. Perrins, editors. Evolutionary Ecology. University Park Press, Baltimore, Maryland, USA.

Krebs, J. R. 1973. Social learning and the significance of mixed-species flocks of chickadees (Parus spp.). Canadian Journal of Zoology 51: 1275-1288.

_____. 1978. Optimal foraging: decision rules for predators. Pages 23-63 in J. R. Krebs and N. B. Davies, editors. Behavioural ecology: an evolutionary approach. Sinauer Associates, Sunderland, Massachusetts, USA.

_____, M. H. MacRoberts, and J. M. Cullen. 1972. Flocking and feeding in the great tit Parus major--an experimental study. Ibis 114: 507-530.

Kroodsma, D. E. 1977. Correlates of song organization among North American wrens. American Naturalist 111: 995-1008.

Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, London, England.

_____. 1968. Ecological adaptations for breeding in birds. Methuen, London, England.

_____ and R. E. Moreau. 1965. Clutch size in tropical passerine birds of forest and savanna. Oiseau 35, supplement: 75-89.

Lawton, R. and V. Dryer. 1980. The vegetation of the Monteverde cloud forest reserve. Brenesia 18: 101-116.

Levings, S. C. and D. M. Windsor. 1982. Seasonal and annual variation in litter arthropod populations. Pages 355-387 in E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, editors. The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington D. C., USA.

Levins, R. 1968. Evolution in changing environments. Monographs in Population Biology 2: 1-120.

Lind, H. 1965. Parental feeding in the oystercatcher (Haematopus o. ostralegus (L.)). Dansk Ornithologisk Forenings Tidsskrift 59: 1-31.

Loiselle, B. A. and W. G. Hoppes. 1983. Nest predation in insular and mainland lowland rainforest in Panama. Condor 85: 93-95.

MacArthur, R. H. 1972. Geographical ecology. Princeton University Press, Princeton, New Jersey, USA.

_____ and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

Marcotullio, P. J. and F. B. Gill. 1985. Use of time and space by Chestnut-backed Antbirds. Condor 87: 187-191.

Marr, T. G. and R. J. Raitt. 1983. Annual variation in patterns of reproduction of the Cactus Wren (Campylorhynchus brunneicapillus). Southwestern Naturalist 28: 149-156.

Martin, R. F. 1981. Reproductive correlates of environmental variation and niche expansion in the Cave Swallow in Texas. Wilson Bulletin 93: 506-518.

Maurier, B. A. and R. C. Whitmore. 1981. Foraging of five bird species in two forests with different vegetation structures. Wilson Bulletin 93: 478-490.

Mayr, E. 1965. The nature of colonizations in birds. Pages 29-47 in H. G. Baker and G. L. Stebbins, editors. The genetics of colonizing species. Academic Press, New York, New York, USA.

Miller, R. S. 1967. Pattern and process in competition. Advances in Ecological Research 4: 1-74.

Morse, D. H. 1968. A quantitative study of foraging of male and female spruce-woods warblers. Ecology 47: 779-784.

_____. 1971. The insectivorous bird as an adaptive strategy. Annual Review of Ecology and Systematics 2: 177-200.

_____. 1974. Niche breadth as a function of social dominance. American Naturalist 108: 818-830.

_____. 1977. The occupation of small islands by passerine birds. Condor 79: 399-412.

_____. 1980. Behavioral mechanisms in ecology. Harvard University Press, Cambridge, Massachusetts, USA.

Morton, E. S. and S. M. Farabaugh. 1979. Infanticide and other adaptations of the nestling Striped Cuckoo Tapera naevia. Ibis 121: 212-213.

Murphy, G. S. 1968. Pattern in life history and the environment. American Naturalist 102: 390-404.

Murray, K. G., K. Winnett-Murray, and G. L. Hunt, Jr. 1980. Egg neglect in Xantus' Murrelet. Proceedings of the Colonial Waterbird Group, 1979: 186-195.

_____, _____, Z. A. Eppley, G. L. Hunt, Jr., and D. B. Schwartz. 1983. Breeding biology of the Xantus' Murrelet. Condor 85: 12-21.

Norton-Griffiths, M. 1967. Some ecological aspects of the feeding behaviour of the oystercatcher (Haematopus ostralegus) on the edible mussel (Mytilus edulis). Ibis 109: 412-424.

O'Connor, R. J. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? Animal Behaviour 26: 79-96.

Oniki, Y. 1979. Is nesting success of birds low in the tropics? Biotropica 11: 60-69.

Orians, G. H. 1961. The ecology of blackbird (Agelaius) social systems. Ecological Monographs 31: 285-312.

_____ and N. E. Pearson. 1979. On the theory of central place foraging. Pages 155-177 in D. J. Horn, G. R. Stairs, and R. D. Mitchell, editors. Analysis of ecological systems. Ohio State University Press, Columbus, Ohio, USA.

Parsons, J. 1975. Asynchronous hatching and chick mortality in the Herring Gull Larus argentatus. Ibis 117: 517-520.

Parsons, P. A. 1983. The evolutionary biology of colonizing species. Cambridge University Press, New York, New York, USA.

Partridge, L. 1976. Individual differences in the feeding efficiencies and feeding preferences of captive great tits. Animal Behaviour 24: 230-240.

Perrins, C. M. 1965. Population fluctuations and clutch-size in the Great Tit, Parus major L. Journal of Animal Ecology 34: 601-647.

Peters, J. L. 1931. Check list of birds of the world. Harvard University Press, Cambridge, Massachusetts, USA.

Pianka, E. R. 1970. On r- and K- selection. American Naturalist 104: 592-597.

_____. 1972. r and K selection or b and d selection. American Naturalist 106: 581-588.

Pitelka, F. A., P. O. Tomich, and G. W. Treichel. 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. Ecological Monographs 25: 85-117.

Powell, G. V. N. 1979. Structure and dynamics of interspecific flocks in a neotropical mid-elevation forest. Auk 96: 375-390.

Preston, F. W. 1962. The canonical distribution of commonness and rarity. Part II. Ecology 43: 410-432.

Rabenold, K. N. 1984. Cooperative enhancement of reproductive success in tropical wren societies. Ecology 65: 871-885.

Raitt, R. J. and J. W. Hardy. 1979. Social behavior, habitat, and food of the Beechey Jay. Wilson Bulletin 91: 1-15.

Remsen, J. V., Jr. and T. A. Parker, III. 1984. Arboreal dead-leaf-searching birds of the neotropics. Condor 86: 36-41.

Ricklefs, R. E. 1965. Brood reduction in the Curve-billed Thrasher. Condor 67: 505-510.

_____. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions in Zoology 9: 1-48.

_____. 1970. Clutch size in birds: outcome of opposing predator and prey adaptations. Science 168: 599-600.

_____. 1977. On the evolution of reproductive strategies in birds: reproductive effort. American Naturalist 111: 453-478.

_____. 1980. Geographic variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97: 38-49.

Robinson, M. H. and B. Robinson. 1970. Prey caught by a sample population of the spider Argiope argentata (Araneae: Araneidae) in Panama: a year's census data. Zoological Journal of the Linnaean Society 49: 345-358.

Robinson, S. K. 1986. Three-speed foraging during the breeding cycle of Yellow-rumped Caciques (Icterinae: Cacicus cela). Ecology 67: 394-405.

_____ and R. T. Holmes. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology 63: 1918-1931.

_____ and _____. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. Auk 101: 672-684.

Rogers, L. E., W. J. Hinds, and R. L. Buschbom. 1976. A general weight vs. length relationship for insects. Annals of the Entomological Society of America 69: 387-389.

Root, R. B. 1964. Ecological interactions of the Chestnut-backed Chickadee following a range extension. Condor 66: 229-238.

_____. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecological Monographs 37: 317-350.

Rowley, I. 1965. The life history of the Superb Blue Wren, Malurus cyaneus. Emu 64: 251-297.

Royama, T. 1966. Factors governing feeding rates, food requirement, and brood size of nestling great tits Parus major. Ibis 108: 315-347.

_____. 1970. Factors governing the hunting behaviour and selection of food by the great tit (Parus major L.). Journal of Animal Ecology 39: 619-668.

Schaffer, W. M. 1974. Optimal reproductive effort in fluctuating environments. American Naturalist 108: 783-790.

Schoener, T. 1971. On the theory of feeding strategies. Annual Review of Ecology and Systematics 2: 369-404.

Schowalter, T. D. 1985. Adaptations of insects to disturbance. Pages 235-252 in S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Sealy, S. G. 1980. Reproductive responses of Northern Orioles to a changing food supply. Canadian Journal of Zoology 58: 221-227.

Selander, R. K. 1964. Speciation in wrens of the genus Campylorhynchus. University of California Publications in Zoology 74: 1-305.

Serventy, D. L. 1971. Biology of desert birds. Pages 287-331 in D. S. Farner and J. R. King, editors. Avian Biology, Volume I. Academic Press, New York, New York, USA.

Shopland, J. M. 1985. Facultative following of mixed-species flocks by two species of neotropical warbler. Ph. D. Dissertation, the University of Chicago, Chicago, Illinois, USA.

Siegel, S. 1956. Nonparametric statistics: for the behavioral sciences. McGraw-Hill Book Company, New York, New York, USA.

Simberloff, D. S. and E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. Ecology 50: 278-295.

_____ and _____. 1970. Experimental zoogeography of islands: a two year record of colonization. Ecology 51: 934-937.

Simpson, E. H. 1949. Measurement of diversity. Nature 163: 688.

Skutch, A. F. 1940. Social and sleeping habits of Central American wrens. Auk 57: 293-312.

_____. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91: 430-455.

_____. 1953. Life history of the southern house wren. Condor 55: 121-149.

_____. 1954. Life histories of Central American birds. Pacific Coast Avifauna 31: 1-448.

_____. 1960. Life histories of Central American birds, II. Pacific Coast Avifauna 34: 116-210.

_____. 1966. A breeding bird census and nesting success in Central America. Ibis 108: 1-16.

_____. 1967. Adaptive limitation of the reproductive rate of birds. Ibis 109: 579-599.

_____. 1972. Studies of Central American tropical birds. Publications of the Nuttall Ornithological Club 10: 159-163.

_____. 1981. New studies of tropical american birds. Publications of the Nuttall Ornithological Club 19: 1-281.

_____. 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. Ornithological Monographs 36: 575-594.

Slagsvold, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. Oecologia 54: 159-169.

_____. 1984. Clutch size variation of birds in relation to nest predation: on the cost of reproduction. Journal of Animal Ecology 53: 945-954.

Slud, P. 1964. The birds of Costa Rica: distribution and ecology. Bulletin of the American Museum of Natural History 128: 283-294.

Smith, N. G. 1980. Some evolutionary, ecological, and behavioral correlates of communal nesting by birds with wasps or bees. Proceedings of the 17th International Ornithological Congress: 1199-1205.

Smythe, N. 1982. The seasonal abundance of night-flying insects in a neotropical forest. Pages 309-318 in E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, editors. The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington D. C., USA.

Snow, D. K. and B. K. Snow. 1963. Breeding and the annual cycle in three Trinidad thrushes. Wilson Bulletin 75: 27-41.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Company, San Francisco, California, USA.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46: 337-366.

_____. 1978. Ecological methods, with particular reference to the study of insect populations. 2nd edition. Chapman and Hall, London, England.

Stacey, P. B. and C. E. Bock. 1978. Social plasticity in the Acorn Woodpecker. Science 202: 1298-1300.

Stearns, S. C. 1976. Life history tactics: a review of the ideas. Quarterly Review of Biology 51: 3-47.

_____. 1977. The evolution of life history traits: a critique of the theory and a review of the data. Annual Review of Ecology and Systematics 8: 145-171.

Stiles, E. W. 1978. Avian communities in temperate and tropical alder forests. Condor 80: 276-284.

Swanberg, P. O. 1981. The clutch-size of the Scandanavian Thick-billed Nutcracker Nucifraga c. caryocatactes influenced by previous year's hazelnut hoard. Vär Fagelvärld 40: 399-408.

Tanaka, L. K. and S. K. Tanaka. 1982. Rainfall and seasonal changes in arthropod abundance on a tropical oceanic island. Biotropica 14: 114-123.

Terborgh, J., J. Faaborg, and H. J. Brockmann. 1978. Island colonization by lesser Antillean birds. Auk 95: 59-72.

Tinbergen, L. 1960. The natural control of insects in pine woods. I. Factors influencing the intensity of predation by songbirds. Archives Neerlandaises de Zoologie 13: 265-343.

Van Valen, L. 1978. The statistics of variation. Evolutionary Theory 4: 33-43.

Vassallo, M. I. and J. C. Rice. 1982. Ecological release and ecological flexibility in habitat use and foraging of an insular avifauna. Wilson Bulletin 94: 139-155.

Verner, J. 1965. Breeding biology of the Long-billed Marsh Wren. Condor 67: 6-30.

Village, A. 1981. The diet and breeding of Long-eared Owls in relation to vole numbers. Bird Study 28: 215-224.

Von Brömssen, A. and C. Jansson. 1980. Effects of food addition to Willow Tit Parus montanus and Crested Tit P. cristatus at the time of breeding. Ornis Scandinavica 11: 173-178.

Welter, W. A. 1935. The natural history of the long-billed marsh wren. Wilson Bulletin 47: 3-34.

Werner, E. E. and D. J. Hall. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60: 256-264.

Wesolowski, T. 1983. The breeding ecology and behaviour of Wrens Troglodytes troglodytes under primeval and secondary conditions. Ibis 125: 499-515.

Westmoreland, D., L. B. Best, and D. E. Blockstein. 1986. Multiple brooding as a reproductive strategy: time-conserving adaptations in mourning doves. Auk 103: 196-203.

Whittaker, R. H. 1975. Communities and ecosystems. Second edition. Macmillan Publishing Company, New York, New York, USA.

_____ and D. Goodman. 1979. Classifying species according to their demographic strategy. I. Population fluctuations and environmental heterogeneity. American Naturalist 113: 185-200.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66: 1211-1214.

Wiley, R. H. 1974. Evolution of social organization and life history patterns among grouse. Quarterly Review of Biology 49: 201-227.

_____ and K. N. Rabenold. 1984. The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. Evolution 38: 609-621.

_____ and M. S. Wiley. 1980. Spacing and timing in the nesting ecology of a tropical blackbird: comparison of populations in different environments. Ecological Monographs 50: 153-178.

Willis, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecological Monographs 44: 153-169.

_____. 1979. The composition of avian communities in remanescent woodlots in southern Brazil. Papéis Avulsos Zoologia, S. Paulo 33: 1-25.

Wittenberger, J. F. 1982. Factors affecting how male and female Bobolinks apportion parental investments. Condor 84: 22-39.

Wolda, H. 1978a. Seasonal fluctuations in rainfall, food, and abundance of tropical insects. Journal of Animal Ecology 47: 369-381.

_____. 1978b. Fluctuations in abundance of tropical insects. American Naturalist 112: 1017-1045.

_____. 1979. Abundance and diversity of Homoptera in the canopy of a tropical forest. Ecological Entomology 4: 181-190.

_____. 1980. Seasonality of tropical insects. I. Leafhoppers (Homoptera) in Las Cumbres, Panama. Journal of Animal Ecology 49: 277-290.

Wong, M. 1986. Trophic organization of understory birds in a Malaysian dipterocarp forest. Auk 103: 100-116.

Wunderle, J. M., Jr. and K. H. Pollock. 1985. The bananaquit-wasp nesting association and a random choice model. Ornithological Monographs 36: 595-603.

BIOGRAPHICAL SKETCH

Kathy Ann Winnett was born in Los Angeles, California, on November 4, 1954. Her early interests in animals, science, and conservation led to her choice of a biology major when she began her college career at the University of California, Irvine, in 1972. After a brief and tedious foray into laboratory work, during which she measured thousands of ant heads, Kathy got her first taste of field biology helping with studies of seabirds on the California Channel Islands, and became permanently hooked. In 1976, she received her Bachelor of Science degree in biological sciences and began graduate school at California State University, Northridge. She continued seabird research in the Channel Islands for three years. Her master's thesis, completed in 1979, investigated the functional significance of habitat selection in Western Gulls (Larus occidentalis). But it was while studying Xantus' Murrelets (Brachyrampus endomychura) on the moonlit, cactus-covered cliffs of Santa Barbara Island, that she fell in love with Greg Murray, another rabid field biologist. They were married between master's degrees in 1979, honeymooned during a summer of field work on seabirds nesting on St. Paul Island in the Bering Sea, and moved to Florida to begin work on their doctorates.

While a graduate student at the University of Florida, Kathy developed diverse interests in ecology, behavior, evolution, and

conservation biology. In 1981, she participated in the Tropical Biology program of the Organization for Tropical Studies and began 2 1/2 years of field work on the comparative behavioral ecology of four species of neotropical wrens in Costa Rica. A year after their return to the U.S., Kathy and Greg produced a son, Dylan. Currently, Kathy tries to maintain her interests in photography, weaving, and birding while juggling, and sometimes mixing, parenthood and biology.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John William Hardy, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Michael W. Collopy
Associate Professor of Forest Resources and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Martha L. Crump
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John H. Kaufmann
Professor of Zoology

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December 1986

Dean, Graduate School